NEURAL REPRESENTATIONS OF CLOSE OTHERS ACROSS ADULTHOOD; EMPIRICAL RESULTS AND APPLICATION OF AN ATTACHMENT THEORETICAL FRAMEWORK

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NEURAL REPRESENTATIONS OF CLOSE OTHERS ACROSS ADULTHOOD; EMPIRICAL RESULTS AND APPLICATION OF AN ATTACHMENT THEORETICAL FRAMEWORK

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Four papers investigate the neural signatures of close other representations in young and older adults. The first paper connects neuroimaging and attachment theory within a novel social, cognitive, and affective framework. Attachment theory is applied to understand why we would expect cognitive representations of close others to be different from other social neural representations. Existing neuroimaging literature on close other representations is examined, highlighting the recruitment of neural systems supporting reward, motivation, and distress alleviation, in addition to the mirror neuron system, default network, and salience network. Methodologies of past studies are reviewed, revealing a diverse array of self-report measures assessing closeness and social cognitive tasks that, taken together, preclude meaningful synthesis of findings. Specific behavioral measures of attachment are discussed, with recommendations for the field. The second paper examines the neural representation of known others along a continuum of attachment using fMRI. Heterosexual adults in romantic relationships for more than two years, made trait judgments for various social targets. Across conditions, trait judgments engaged the default network and lateral prefrontal cortex. Judgments about oneself and a partner were associated with a common activation pattern encompassing anterior and middle cingulate, posterior superior temporal sulcus, as well as anterior insula. These results

provide novel evidence that mentalizing about known familiar others results in differential brain activity and that adult attachment is a distinguishing feature of these differences. The third paper investigates the neural representation of known others in young and older adults, using the same trait judgment fMRI paradigm. Across both age groups, all trait judgments engaged default network regions such as dorsal and ventral medial prefrontal cortex and posterior cingulate cortex; however, older adults showed a lack of neural differentiation between social conditions. Both age groups demonstrated connectivity between dorsal and ventral medial prefrontal cortex and other default network regions during trait judgments. However, older but not young adults also showed increased functional coupling between medial and lateral prefrontal brain regions. Results extend the dedifferentiation and default – executive coupling accounts of neurocognitive aging to social aging neuroscience. The fourth paper examines the neural representation specifically of parents and adult children, again using a trait judgment task in fMRI. Higher levels of parent and child attachment were associated with lower neural recruitment in anterior cingulate cortex, amygdala, posterior cingulate cortex, medial temporal lobe, and occipital face area. Results provide novel evidence for neural signatures of chronic accessibility, as bringing to mind one's attached parent or child requires less engagement of brain regions involved in distress relief, memory, and facial processing. Taken together, the present studies utilize fMRI methods to contribute to an emergent neuroscience of close relationships and attachment.

BIOGRAPHICAL SKETCH

Anne C. Laurita graduated from West Morris Mendham High School in Mendham, New Jersey, in 2010. She received her B.S. in Human Development from the College of Human Ecology at Cornell University in 2013. Her major concentration was Social and Personality Development, and she completed a minor History of Art in the College of Arts and Sciences. She then received her M.A. in Developmental Psychology in 2015 and her Ph.D. in Developmental Psychology in 2017 from Cornell University. Her research investigates the topic of neural, cognitive, and behavioral markers associated with close social relationships, specifically using functional magnetic neuroimaging to understand how mental representations of adult attachment figures reflect the structure and function of underlying neural networks. Her work was partially funded by the College of Human Ecology, under a Martha Foulk Fellowship. As a graduate student, she conducted research across the Adult Attachment Laboratory under Cindy Hazan and the Laboratory of Brain and Cognition under Nathan Spreng. She also served as a Graduate Resident Fellow since 2013 in Alice H. Cook House on West Campus, Cornell's residential college system. Laurita will join the Skorton Center for Health Initiatives at Cornell Health as a post-doctoral fellow in Summer 2017. She hopes to pursue a career integrating current methods in public health and psychology research with college health promotion initiatives.

For F&F, "To reach the unreachable star!"

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CHAPTER 1

Introduction

As members of a highly social species, humans form and maintain close social relationships throughout the life course. These unique, stable relationships are often conceptualized as attachment bonds (Bowlby, 1973, 1982) and are associated with feelings of security conferred by attachment figures' presence (Bowlby, 1982; Mikulincer & Shaver, 2007a; Sroufe & Waters, 1977). Attachment theory posits that, in infancy, proximity maintenance to a primary caregiver is necessary for survival (Bowlby, 1982). This theoretical model has since been extended to explain attachments in adulthood, as well (Hazan & Shaver, 1987). The overarching attachment framework serves as a predominant paradigm for understanding the regulatory powers of our closest social bonds and the psychological and physiological health benefits conferred by these relationships (Hazan, Gur-Yaish, & Campa, 2004; Pietromonaco, Feldman Barrett, & Powers, 2006).

However, physical proximity is not always needed for felt security; once one forms a mental representation of an attachment figure, he or she can utilize this same system of behavioral dynamics from that cognitive representation alone. The chronic accessibility of attachment figure mental representations (Andersen & Cole, 1990; Baldwin et al., 1996)—by which these representations are easily brought to mind and utilized—comes about due to learning and conditioning under the inborn system of attachment bonding. Mental representations of attachment figures, being chronically accessible and highly relevant for emotion-regulation, are inherently different from representations of others — acquaintances, friends, or even ourselves (Mikulincer & Shaver, 2007a; Pietromonaco, Feldman Barrett, & Powers, 2006). Attachment figure mental representations are, for one, often used effectively in

response to stressors (e.g., Coan, Schaefer, & Davidson, 2006; Grewen et al., 2003; Eisenberger et al., 2011; Selcuk et al., 2013). Importantly, there is growing evidence to support the notion that these cognitive representations of our closest relationship partners are also associated with unique patterns of brain response (e.g., Acevedo et al., 2012; Krienen, Tu, & Buckner, 2010).

The present dissertation aims to advance our understanding of the neural signatures of close other representations, across adulthood. Chapter 2 reviews existing literature on close other representations, connecting neuroimaging and attachment theory within a novel social, cognitive, and affective framework. Attachment theory is discussed and applied to understand why we would expect cognitive representations of close others to be different from other social representations in the brain. This review highlights the recruitment of neural systems supporting reward, motivation, and distress alleviation, in addition to the mirror neuron system, default network, and salience network; critically examines the diverse methodologies of past studies; and provides recommendations for the field. Chapter 3 examines the neural representation of known others along a continuum of closeness using functional magnetic neuroimaging (fMRI) in young adults. This study provides one of the first pieces of evidence that mentalizing about known others results in differential brain activity and that adult attachment is a distinguishing feature of these differences.[1] Chapter 4 again utilizes fMRI to investigate the neural

[1] Chapter 3 was previously published in the journal Social Cognitive & Affective Neuroscience (SCAN) (Copyright © 2017 by Oxford University Press. Reproduced with permission. The official citation that should be used in referencing this material is: Laurita, A.C., Hazan, C. & Spreng, R.N. (2017). Dissociable patterns of brain activity for mentalizing about known others: A role for attachment. Social Cognitive & Affective Neuroscience. No further reproduction or distribution is permitted without written permission from Oxford University Press).

representation of known others in both young and older adults. Findings demonstrate various interactions between aging and the representation of social closeness; for one, neural representations of close others become less differentiated in older adulthood. This study is one of the first to extend the dedifferentiation and default – executive coupling accounts of neurocognitive aging to social neuroscience. Chapter 5 uses fMRI to examine the neural representation of parents and adult children, looking specifically at how degree of attachment to these figures modulates associated brain activity. Results provide novel evidence for unique neural signatures of chronic accessibility, as bringing to mind one's attached parent or child requires less engagement across a variety of brain regions. Finally, Chapter 6 discusses directions for future research on the neural representation of close others. Overall, the present studies utilize fMRI methods to contribute to an emergent neuroscience of close relationships and attachment.

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CHAPTER 2

An Attachment Theoretical Perspective for the Neural Representation of Close Others

> I love you without knowing how, or when, or from where,
> I love you straightforwardly, without complexities or pride;
> so I love you because I know no other way
>
> than this: where *I* does not exist, nor *you*,
> so close that your hand on my chest is my hand,
> so close that your eyes close as I fall asleep.
>
> -Pablo Neruda, One Hundred Love Sonnets: XVII, 1959;
> Translated by Stephen Tapscott

If you are able to suspend disbelief for a moment, assume that two individuals' bodies could so precisely synchronize as a function of mere affection. Then perhaps Neruda's prose does accurately reflect feelings of intense love. His imagery evokes a level of intimacy and connection reserved only for certain close relationships. Humankind's fascination with the experience of love and thinking about loved-ones stretches far back through history, long before Neruda wrote his sonnets. This curiosity flourishes today, too; the observation of biobehavioral synchrony, or the sensitization to and mirroring of another's physiological and behavioral cues, in pair bonds (see Feldman, 2016, for review), for instance, provides intriguing support for this particular poetic musing. Across scientific domains we are relatively new to the formal exploration of close social bonds. Yet, we have already made great strides in amassing evidence for these unique attachment relationships that are operative across the lifespan and manifest in affect, behavior, cognition, and physiology.

From an ethological perspective, interest in investigating close relationships stems from knowledge of the social pressures unique to the human species, such as navigation of complex social hierarchies and formation of successful mating relationships (see Fletcher et al., 2015, for review). Our ability to cognitively represent others and respond accordingly differentiates us

from our primate relatives (Tomasello, 1999). Evolutionary theorists postulated the social brain hypothesis to account for humans' unique social-cognitive skills. As humans evolved, living in group settings, individuals had to manage increasing complexity and number of social relationships. This evolutionary pressure was associated with markedly larger brains (Dunbar, 1998). The capacity to successfully navigate through personal interactions remains crucial for human survival. We understand that the formation and maintenance of close relationships is essential for defining one's sense of self (Vygotsky, 1978), surviving to mate and raise young (Buss & Schmitt, 1993), and bolstering physical and mental health throughout the lifespan (Cohen, 2004; Cornwell & Waite, 2009; House, Landis, & Umberson, 1988; Kiecolt-Glaser & Newton, 2001). The ability to stratify personal relationships—differentiating close from other more distal connections across social networks—is especially important for successful social navigation.

Social-cognitive neuroscientists have begun to map this "social landscape" to the complex architecture of the brain. Patterns of neural activity have been identified that differentiate cognitive representations of close others from less-close others (e.g. Krienen, Tu, & Buckner, 2010). Yet, efforts to integrate social psychology and neuroscience research to define how one neurally represents close others have proven challenging; there are several persistent barriers, including the absence of a common theoretical framework, disparate research methods, and measurement challenges. In order to use measures of brain activity to make inferences about close other representations in the brain, the emerging field of close relationship neuroscience needs to make progress toward clearer measurements and evaluation of constructs defining close relationships. The present review connects past work, providing a common framework for understanding neural representations of close social relationship partners. We aim to show how

clear integration of a few, central concepts across the relevant bodies of literature provides a novel perspective for the emergent field of close relationship neuroscience and provides a path for future inquiry.

Outline and Scope of the Present Review

The primary objective of this review is to provide an integrated common framework for understanding the neural representation of our closest social relationships. We begin with a survey of the theoretical and social psychological bases of attachment, examining how they inform social neuroscience research. We emphasize the potential for attachment theory to guide functional neuroimaging investigations of close other mental representations. The hallmark of attachment bonds is the feeling of security associated with attachment figures' availability. Attachment theory suggests that behavior towards a certain close other differs fundamentally from behavior towards more distant others, signaling that neural representations of social others may be similarly stratified across a proximal-distal continuum. Utilizing criteria provided by attachment theory, by stratifying social relationships by self report of felt security, could provide the necessary framework to differentiate the corresponding neural representations. Attachment theory can provide neuroscientists with specific behavioral and cognitive constructs to examine.

We next present recent and seminal social cognitive neuroscience studies which have implicated a wide array of brain regions in representing close relationships including: the dopaminergic and opioid reward systems; the limbic system in emotional regulation and distress alleviation; the mirror neuron system; the default network, responsible for internally-directed thought and social cognition; and the salience network in differentiation of unique close other representations. The studies we review adopted diverse approaches to operationalize and measure the construct of close other representations. In the next section of our review, we

evaluate these approaches. We discuss core methodological challenges in this area, including: use of terminology relating to close relationships and to attachment bonds; assessment of relationship length; use of self-report measures of relationship closeness and quality; differing neuroimaging task paradigms; and the potential impact of demographic factors such as sex, sexual orientation, and age. Of particular interest are experimental parameters reflecting how researchers measure "closeness" of close others in relation to neural responses. Such methodological discrepancies preclude meaningful integration of findings across concepts and fields. To conclude, we offer a series of recommendations designed to promote an interdisciplinary approach for mapping the neural representation of unique close relationships, conceptualized as attachment bonds. We review behavioral methods to assess attachment and close adult relationships with recommendations for the field. Developing reliable markers of attachment, grounded in social psychological theory, is a critical step in mapping close relationship representations in the human brain.

As this inquiry comes at a critical time for close relationship neuroscience (see Feldman, 2017, for review; Laurita, Hazan, & Spreng, 2017), we seek to situate this work within a broader context of the disparate fields upon which it draws. First, we focus this review solely on close relationships in adulthood, gathering evidence primarily from studies of adult romantic relationships and secondarily from studies of parent/adult-child relationships or close adult friendships. We do not review studies of infants' or children's close relationships, nor do we review studies of clinical populations, adult or otherwise. Second, we utilize attachment theory as a normative, quantitative framework for our discussion. Motivated by Bowlby's (1973) traditional model, our perspective hinges on the quantifiable presence (versus non-presence) of attachment to characterize close relationships. We do not approach attachment theory from

Ainsworth and colleagues' (1978) tradition of observing attachment style; researchers have yet to integrate relationship-observational methods with collection of neuroimaging data, and we do not yet have sufficient data to delve into such individual differences. Third, we use specific language, discussing "close other representations" as a unifying construct throughout our review of results and methods from existing research. Towards the end of this work, we apply the theoretical framework of attachment theory and incorporate references, where useful, to "adult attachment figure representations", concretely illustrating the boundaries of our framework. We avoid appropriating terminology from clinical or developmental domains, whose language is too-often conflated with that from other related disciplines. Fourth, we draw exclusively from the body of work using blood oxygen level dependent (BOLD) functional magnetic neuroimaging (fMRI). Most existing research on the neuroscience of human social relationships has used this method to gain spatial and temporal information about brain function in response to social stimuli. Within this coarse methodological focus, we parse out different results by calling attention to differing backgrounds and smaller methodological choices, such as specific fMRI tasks and contrasts used. We made these choices to narrow our focus and to avoid confusing concepts or findings from traditionally disparate areas of research.

We conclude by proposing a standardized battery of relationship measures, consistent with the tenets of attachment theory. We argue that standardized assessments, including measures of attachment status, style, and relationship quality, are necessary to develop comprehensive, reliable, and replicable representations of real-world attachment bonds.

Utility of the Adult Attachment Framework

Within the attachment literature—across studies of infants' primary caregivers and adults' romantic partners—one hallmark of these unique, close social bonds is the feeling of security,

and concomitant affect-regulatory benefits, associated with attachment figures' presence (Bowlby, 1973; Mikulincer & Shaver, 2007a; Sroufe & Waters, 1977). Bowlby (1973) initially theorized that the function of attachment for infants was to support maintenance of proximity with a primary caregiver. Lack of perceived proximity and the accompanying distress activates this system, whereas comfort and the ability to explore is achieved through this system of attachment behavioral dynamics (Bowlby, 1973). These relationships are therefore characterized by four behavioral "features": proximity seeking, separation distress, safe haven, and secure base (Mikulincer & Shaver, 2007a). Observational studies of young children were the first to demonstrate the important role of attachment figures in pacifying separation-related distress upon reunion (Ainsworth et al., 1978). Ainsworth's work paved the way for a research tradition of examining individual differences in patterns of behavioral response, observed and noted as "attachment styles".

Attachment theory has since been extended to explain certain close, romantic relationships in adulthood (Hazan & Shaver, 1987). The overarching adult attachment framework serves as a predominant paradigm for understanding the regulatory powers of our closest social bonds (Hazan, Gur-Yaish, & Campa, 2004; Pietromonaco, Feldman Barrett, & Powers, 2006) and the long-term psychological and physiological health benefits conferred by these relationships (e.g., Beck et al., 2013). However, physical proximity is not always needed for felt security; once one has a mental representation of an attachment figure (also known as an internal working model), he or she is inherently shaping expectations, behaviors, and utilization of this system on that cognitive representation. The so-called "chronic accessibility" of attachment figure mental representations (Andersen & Cole, 1990; Baldwin et al., 1996)—by which these representations are not just rich and detailed in content but also quick to be recalled

and utilized—comes about due to learning and conditioning under this inborn system of attachment bonding, operative across the lifespan.

Since cognitive representations of attachment figures are thought be chronically accessible and relevant for emotion-regulation, they are inherently different in content and utilization from representations of others — acquaintances, friends, or even ourselves (Mikulincer & Shaver, 2007a; Pietromonaco, Feldman Barrett, & Powers, 2006). Mental representations of close others in adulthood are composed of highly salient social memories and, often, function independent of context. In early development, parents serve as our primary attachment figures; in young adulthood and beyond, romantic partners will often serve this role (Hazan et al., 1991; Hazan & Zeifman, 1999; Nickerson & Nagle, 2005). Repeated utilization of romantic partner mental representations is important for the maintenance of long-term, mutually-beneficial pair bonds (Mikulincer & Shaver, 2007a).

Within the context of pair bonds, romantic partner mental representations have been further conceptualized as cognitive expansions of the self (Aron & Aron, 1986). Cognitive representations of attachment figures play a role in the pursuit of partner-specific interpersonal goals (Fitzsimons & Bargh, 2003) and in intertwining the cognitive and emotional contexts of both relationship partners (Zayas, Shoda, & Ayduk, 2002). Moreover, these representations can influence our perceptions of, and responses to, others in our social world through a process known as social-cognitive transference (Andersen & Cole, 1990). Experimental studies (e.g., Günaydin et al., 2012) demonstrate the occurrence of social-cognitive transference, in which internal working models of close others can actually influence how novel social stimuli are perceived and encoded. The theory of social-cognitive transference proposes that mental

representations of attachment figures strongly influence how we judge others in our social world (Andersen & Cole, 1990; Günaydin et al., 2012).

Beyond these effects, of great importance are the ramifications of attachment figure mental representation utilization in the face of stressors—at the affective, behavioral, neural, and cognitive levels. Recent research demonstrates that attachment figure mental representations serve various functions contributing to our health and happiness. Just bringing to mind the cognitive representation of one's romantic partner can promote recovery from recalling upsetting autobiographical memories (Selcuk et al., 2012), provide distress alleviation when giving a public speech (Grewen et al., 2003), decrease the neural response to threat with partner hand-holding (Coan, Schaefer, & Davidson, 2006), and reduce the subjective experience of pain, even above one's described pain threshold (Eisenberger et al., 2011). Importantly, we have evidence to support the notion that mental representations are not immutable; representations themselves can be altered, at the levels of cognition, behavior, and the brain, based on felt security (Collins & Feeney, 2004).

Both theoretical and empirical work support the uniqueness of attachment figure representations, especially within the context of romantic relationships. In many cases, the presence of intrinsically rewarding contact comfort and sexual activity indicate that romantic partnerships are uniquely intimate attachment bonds by nature (Zayas, Merrill, & Hazan, 2015). As an attachment bond with a romantic partner forms, this individual becomes integrated into one's cognitive sense of self (Aron & Aron, 1986) and influences one's physiological homeostatic functions (Pietromonaco, DeBuse, & Powers, 2013). Biobehavioral synchrony, or physiological co-regulation, is often present such pair bonds (for review, see Feldman, 2017).

Because of the powerful role of attachment figure mental representations in forming and maintaining close bonds and, more broadly, in assisting individuals with navigation of their social environments, it is likely that these representations have unique neural signatures. We propose that, by utilizing adult attachment criteria, researchers can implement theoretically-driven empirical studies and finer-grained corresponding analyses to differentiate our closest of social relationships representations in the brain. If we apply adult attachment to derive more precise operational definitions of close relationships, we can begin to disentangle the important functional regions and networks of the brain we predict to be recruited in such social cognitive processing.

Diverse Findings from fMRI Studies of Close Other Representations

Close other neural representations have been approached from two distinct fields of thought through use of functional neuroimaging (fMRI) methods. Accordingly, results show diversity in the brain regions and networks, or large-scale systems of functionally connected brain regions, implicated in creating, updating, and utilizing these mental representations. Social neuroscientists focus on motivation and reward conditioning to close others and the affect-regulatory capabilities close others impart. These investigations consistently implicate the recruitment of reward and distress-alleviation systems in the brain (e.g., Acevedo et al., 2012; Bartels & Zeki, 2000; Xu et al., 2011). Cognitive neuroscientists, on the other hand, focus on characterizing the differential cognitive representations of social others. These studies typically investigate how close other representations are created over time through the encoding and retrieval of personal information and the accumulation of social memories. This body of work examines how the brain supports and updates representations of close social others and relates them to representations of the self, repeatedly demonstrating roles for neural systems involved in

memory and internally-directed thought (e.g., Heatherton, et al., 2006, Krienen, Tu, & Buckner, 2010; Wang at al., 2012). The different theoretical and methodological approaches likely result in the varied findings across individual studies of close others neural representations. In the following section, we review existing findings, highlighting several specific studies that have most meaningfully, as evidenced by citations, contributed to our emerging understanding of the neural representation of close others.

Limbic system; Reward pathways and emotion regulation

Limbic system activity plays a critical role in close other mental representations. The mesocorticolimbic and nigrostriatal dopaminergic reward pathways are involved in motivating attachment bond formation and maintenance, by way of conditioning to the presence of a romantic relationship partner (Fisher, Aron, & Brown, 2005). Attachment figure representations become imbued with high reward as positive experiences accumulate with these individuals. Behaviorally, this system manifests as a cycle of attachment features; we seek proximity to those who provide us with a secure base. Existing social neuroscientific literature provides ample support for this facet of close other neural representations, finding recruitment of brain regions such as the ventral tegmental area (VTA), ventral and dorsal striatum, mid-insula, caudate head, and putamen (Acevedo et al., 2012; Aron et al., 2005; Bartels & Zeki, 2000; Inagaki & Eisenberger, 2012; Inagaki et al., 2015; Inagaki et al., 2016; Langeslag et al., 2014; Scheele et al., 2013; Stoessel et al., 2011; Xu et al., 2011; Xu et al., 2012; Zeki & Romaya, 2010).

The topic of early-stage, pre-attachment romantic relationships attracted social neuroscientists once they acquired the tools for BOLD fMRI. Early-stage relationships are associated with feelings of euphoria and heightened neurochemical reward (Aron et al., 2005). Several of the studies above examine early-stage, intense relationships characterized by feelings

of infatuation. In the earliest assessment of the neural basis of romantic love, participants who reported being deeply "in love" were instructed to look at photographs of their romantic partners and of three different friends while in the fMRI scanner (Bartels & Zeki, 2000). Results showed increased activation in medial insula, caudate nucleus, putamen, and anterior cingulate cortex (ACC) when participants looked at their romantic partners' photos. These neural regions are dopamine-rich and are consistently recruited in reward paradigms. This activation pattern was investigated in another sample of participants in early-stage, intense romantic relationships, and increased activations specific to romantic partners were again found in dopamine-rich areas of the brain such as right VTA and medial caudate nucleus (Aron et al., 2005). Individuals "happily in love" in early-stage romantic relationships recruit bilateral insula and ACC more often than those recently separated from a romantic partner (Stoessel et al., 2011). Study participants from an Eastern culture, too, recruit VTA and caudate in representing early-stage romantic partners (Xu et al., 2011). Directing attention toward a beloved, early-stage romantic partner versus a friend has also been associated with increased ventral striatum activity (Langeslag et al., 2014).

The past several years have seen a shift in focus reflecting growing interest in the neuroscience of attachment; recent studies have examined the role of motivation and reward systems in stable, longer-term adult romantic relationships. In 2012, the first and only longitudinal study on this topic examined the progression from early-stage passionate love to longer-term romantic relationships (Xu et al., 2012). Participants included individuals who, at 40-month follow-up, were together with their romantic partners from the first assessment and others who had since broken up. Results showed that partner-related activity in the tail of the caudate during the early-stage assessment was associated with remaining together 40 months later, as well as with higher self-reported commitment to the relationship. A second, somewhat

counterintuitive set of activational effects also emerged, wherein lower early-stage activity in medial orbitofrontal cortex and nucleus accumbens (NAcc) was associated with greater commitment, happiness, and longevity of participants' relationships at 40-month follow-up. The directionality of Xu et al.'s (2012) second set of activational effects was brought into question by another foundational study of long-term relationship representations. Acevedo and colleagues (2012) made an important advance, examining neural representations of long-term romantic partners, using a photo-viewing paradigm. They found that individuals who reported high, passionate love for a long-term spouse showed significant patterns of neural activation in response to partner images versus acquaintance images in the VTA and substantia nigra. Furthermore, the authors found that greater closeness—measured by one specific social-cognitive measure—was related to greater VTA activity in response to partner images versus friend images. Relationship length (here, years married) was positively correlated with activation of NAcc and caudate in response to romantic partner versus friend. There is also evidence that this pattern of findings holds across samples of non-heterosexual individuals in long-term romantic relationships (Zeki & Romaya, 2010).

Other recent research adds breadth to our understanding of the neural reward system's role in representing close others. The neuropeptides oxytocin and vasopressin also interact with dopamine in neural reward processing (Love et al., 2012) and support long-term pair bond formation (e.g., Ditzen et al., 2009; Grewen et al., 2005; Schneiderman et al., 2012). The behavioral and neural effects on response to long-term romantic partners of manipulating individuals' oxytocin levels have been empirically examined (Scheele et al., 2013). In both a discovery and a replication study, either instranasal oxytocin or a placebo was administered to heterosexual male participants in long-term romantic relationships. Oxytocin enhanced the

positive behavioral bias towards romantic partner photos (measured by ratings of attractiveness against objectively matched controls of unfamiliar or familiar others). Further, results showed a parallel neural response, as VTA and NAcc were recruited for romantic partners over unfamiliar others in the discovery study. In the replication study, familiar other faces were introduced as a social control; here, oxytocin similarly enhanced the neural response to partners over familiar others in left NAcc and right putamen.

The regulation of emotion associated with thinking of a close other highlights the role of other neural regions within the limbic system, such as ACC and the insula (Beckes, Coan, & Hasselmo, 2013; Coan, Schaefer, & Davidson, 2006; Eisenberger et al., 2011; Younger et al., 2010). Studies assessing affect regulation often utilized threat paradigms, manipulating participants' anticipation or experience of pain while in the scanner. The experience of threat can be brought on by a variety of experimental stimuli, such as minor electrical shock, hot or cold sensations, uncomfortable pressure applications, or display of anxiety-provoking images or words. Yet, the underlying principle of emotion regulation provided by a close other representation is common to all of these experiments and to adult attachment theory; in the face of stressors, individuals utilize their attachment figure mental representations as safe havens and may show separation distress if this comfort is not available.

Coan, Schaefer, and Davidson conducted their seminal "hand-holding" study in 2006. They examined spouse versus stranger hand-holding when participants were faced with anticipation of a painful experience in the scanner. The authors found activity in several threat-responsive regions of interest; they observed that spousal hand-holding (in other words, spouse-related attenuation of threat) recruited right dorsolateral prefrontal cortex, left caudate, and NAcc, whereas activity in ventral ACC and posterior cingulate cortex (PCC) was shown for both

spouse- and stranger-related attenuation of threat. Using a similar paradigm, modified to tap individuals' abstract mental representations of non- physically present partners, another experiment had female participants view partner versus stranger pictures while receiving painful heat stimulations (Eisenberger et al., 2011). Results showed reduced dorsal ACC and anterior insula and increased ventromedial prefrontal cortex (vmPFC) activation in the partner-picture condition. Additionally, increased vmPFC activity in response to partner photographs was associated with higher perceived support from the partner, longer relationship lengths, reduced subjective ratings of pain, and decreased activity in pain-related neural regions such as ACC and insula. These findings lend support to the safe-haven role of attachment figure neural representations. Attachment figures often serve as safe havens, or responsive people that individuals turn to for comfort in times of distress; the research described above explains the coupling of behavioral responses to attachment figure support with neural reduction of threat and pain.

Several other studies have considered the reversal of roles in affect regulation, investigating how our brains manage perceptions of threat to close others (versus to ourselves). Incorporating elements of emotion regulation research and cognitive neuroscientific methods, one study applied a mild electric shock paradigm to look at self-focused threat, versus close friend-focused threat or stranger-focused threat (Beckes, Coan, & Hasselmo, 2013). Significant conjunctions between the threat-to-self and threat-to-friend conditions were observed in anterior insula, putamen, and supramarginal gyrus. Studies on the process of giving and receiving emotional support to close relationship partners also exemplify the significant emotion-regulatory capacities of attachment figure representations. A series of studies examining support-giving, support-receiving, and even feelings of loneliness further demonstrated the unique

response of the ventral striatum to representations of long-term-romantic partners (Inagaki & Eisenberger, 2012; Inagaki et al., 2015; Inagaki et al., 2016). Taken together, this social neuroscientific research on close other neural representations closely aligns with the tenets of adult attachment theory, moving the field towards an empirically-supported neuroscience of attachment.

Mirror neuron system; Resonance with another's thoughts and feelings

A smaller group of neuroscientists have asserted the potential role of the mirror neuron system (MNS) in representing close others (Ortigue & Bianchi-Demicheli, 2008; Petrican, Rosenbaum, & Grady, 2015). The MNS—in particular, a collection of neurons within premotor cortex—is thought to play an important role in the ability to understand others' actions, both in humans and other primates (for review, see Ortigue, 2010 and Van Overwalle & Baetens, 2009). One context in which the role of the MNS has been assessed was that of neural responsiveness to a spouse's incongruent emotions; presumably, our closest relationships might be characterized by sensitivity to when a partner's feelings may be incongruous with one's own. One recent study examined older adult female participants in long-term marriages, asking them to make trait judgments about either their spouse's or a stranger's affect in the presence of incongruent verbal and non-verbal cues (Petrican, Rosenbaum, & Grady, 2015). Greater activity in putative MNS areas, such as the inferior parietal lobules, was associated only with processing a spouse's, but not a stranger's, non-verbal cues when the target's behavior was positive while in a negative (incongruous) context. Although this line of research shows promise for our growing understanding of the complex role played by the MNS in relating to a close other, there are remaining questions about the interaction of this system with others, such as the default network.

Default network; Mentalization for self and others

Cognitive neuroscientists have consistently found activation within a collection of functionally-connected brain regions known as the default network to be associated with social-other mental representations. Core brain areas within the canonical default network include the medial temporal lobes, medial prefrontal cortex (mPFC), PCC, lateral prefrontal cortex, lateral temporal cortices, and lateral parietal cortices (Buckner & Carroll, 2007; Spreng, Mar, & Kim, 2009). Default network activity is thought to support many aspects of social cognition. As social beings, we use our own experiences to generate social conceptual knowledge which, in turn, allows us to develop and implement strategic social behaviors reliant on default network function (Spreng & Mar, 2012). For example, the integrity of vmPFC predicts the ability to retrieve impressions of others (Cassidy & Gutchess, 2012), and attributional decisions and judgments of others' emotional states recruit vmPFC (Haas, Anderson, & Filkowski, 2015). The default network also enables us to imagine the experiences of others. In one study, participants were taught the personalities (based on two dimensions of agreeableness and extraversion) of four characters (Hassabis et al., 2014). They then imagined those characters' behaviors across different situations. Results showed that activity in the mPFC reliably predicted which characters the participants were imagining. This body of literature has effectively set the stage for cognitive-neuroscientific investigations of specific social dynamics and unique, close social relationships

In studies specific to close other neural representations, regions of interest within the default network include the mPFC and PCC (Gobbini et al., 2004; Heatherton et al. 2006; Krienen, Tu, & Buckner, 2010; Laurita, Hazan, & Spreng, 2017; Mitchell, Macrae, & Banaji 2006; Tacikowski et al. 2011, 2013; Wang et al., 2012). Early work conceptualized social proximity as a function of one of two factors: familiarity or similarity. Participants in the earliest

of these studies viewed faces of personally familiar people (relatives and friends), familiar famous individuals (such as public leaders or actors), and strangers (Gobbini et al., 2004). Viewing personally familiar faces—contrasted against both famous familiar faces and strangers—was associated with a pattern of neural response in bilateral PCC and precuneus. The authors interpreted their results as evidence for close-other "person knowledge" in the brain, supporting past findings implicating these regions in processes such as theory-of-mind- for well-known others. MPFC activity also assisted in differentiating similar-other representations from dissimilar-other representations during a trait-judgement task (Mitchell, Macrae, and Banaji, 2006). More specifically, ventral mPFC was recruited here for self-referential and similar other related thought, whereas more dorsal mPFC regions were active for thought regarding dissimilar others. This finding prompted interest in determining how default network activity supports a kind of "simulation" of the internal mental states of others and how it might selectivity do so for socially proximate others.

Within the literature on mentalizing (or, imagining the thoughts or feelings of others), a few studies have initiated a focus on the role of mPFC and PCC in differentiating close other from stranger or from self representations. Some have asserted that the representation of self is "special", uniquely recruiting mPFC in contrast to representations of intimately known others (e.g., Heatherton et al., 2006). In 2010, Krienen, Tu, and Buckner advanced this earlier work. Participants in their study made judgments about personal preferences in response to facial images of close friends versus strangers. They found, for the first time, that friends versus strangers yielded a network of brain regions including mPFC, PCC/ retrosplenial cortex, inferior parietal lobe, lateral temporal cortex, and medial temporal lobe (Krienen, Tu, & Buckner, 2010).

In the years since this study, further research has provided more nuance to understanding the role of the default network in representing close others. These findings have been extended to collectivistic cultures; thinking of certain close others such as mothers or the self (even over best friends or fathers) in a trait judgment task yielded higher mPFC and ACC activity (Wang et al., 2012). A similar pattern of results has also been found using a target name-viewing paradigm (Tacikowski et al., 2011) and in extending this paradigm across the modalities of viewing and listening to names (Tacikowki et al., 2013).

Considering the rapidly growing evidence for the default network's role in representing close others, we were interested in how this network, as well as other brain regions and networks, may respond to relationships of differential closeness. More specifically, we wanted to learn how the brain might differentially represent those individuals who serve as our primary attachment figures. To begin answering these questions, we recently explored the neural representation of known others along a continuum of attachment using fMRI (Laurita, Hazan, & Spreng, 2017). In this experiment, heterosexual adults in romantic relationships for over two years were asked to make trait judgments for a romantic partner, parent, close friend, familiar acquaintance, and self during an fMRI scan. Across all social-other and the self conditions, in contrast to a motor control condition, trait judgments engaged the default network and lateral prefrontal cortex. Judgments about oneself and attached romantic partner additionally recruited anterior and middle cingulate cortex and anterior insula, relative to parent and close friend. These results provided novel evidence that mentalizing about primary attachment figures—here, romantic partners—engages the default and salience networks. Salience network regions such as anterior cingulate and anterior insula detect internal and external events that are personally meaningful and interact with the default network to represent internal events (Christoff et al., 2016; Uddin et al., 2015).

The results of our study showed this interaction by way of the unique patterns of neural response to attached romantic partners and to the self. We concluded that, while the default network is recruited for construction and utilization of social representations, the salience network selectively attunes us to the most meaningful of these representations—those of primary attachment figures.

Our approach has several innovations for work on known others. First, our experimental stimuli included the names of real individuals who were highly-relevant to each participant. Second, unlike past studies utilizing passive fMRI tasks (such as free-viewing photos of known others), our paradigm required that participants actively mentalize about each of the social targets. Third, we included numerous self-report measures in an attempt to better describe and characterize participants' relationships with their social targets; one such measure, for example, provided us with information about who participants' (primary) attachment figures were. We were able to provide initial evidence that the representation of adult attachment is a distinguishing feature of the neural activation differences in social cognition.

Cortical and subcortical interactions support representation of close others

If one overarching conclusion emerges from fMRI studies of close other representations, it is that we are now arriving at a novel, cross-disciplinary neuroscience of close relationships—yet from several very different perspectives. Just as our mental representations of close others reflect the complexity of rich person-knowledge, emotionally salient memories, and unique regulatory capabilities, the neural regions and networks responsible for carrying close other representations are complex, as well. Bringing together past findings, these neural regions and networks appear to include: dopamine-rich regions sensitive to partner reward such as VTA, NAcc, and putamen; threat-responsive regions sensitive to partner comfort such as ACC and

insula; mirror neuron regions sensitive to a partner's inner states such as inferior parietal lobules; default network regions sensitive to mentalizing about a partner such as mPFC and PCC; and salience network regions sensitive to meaningful cues associated with a partner such as anterior insula and anterior cingulate.

Figure 2.1.

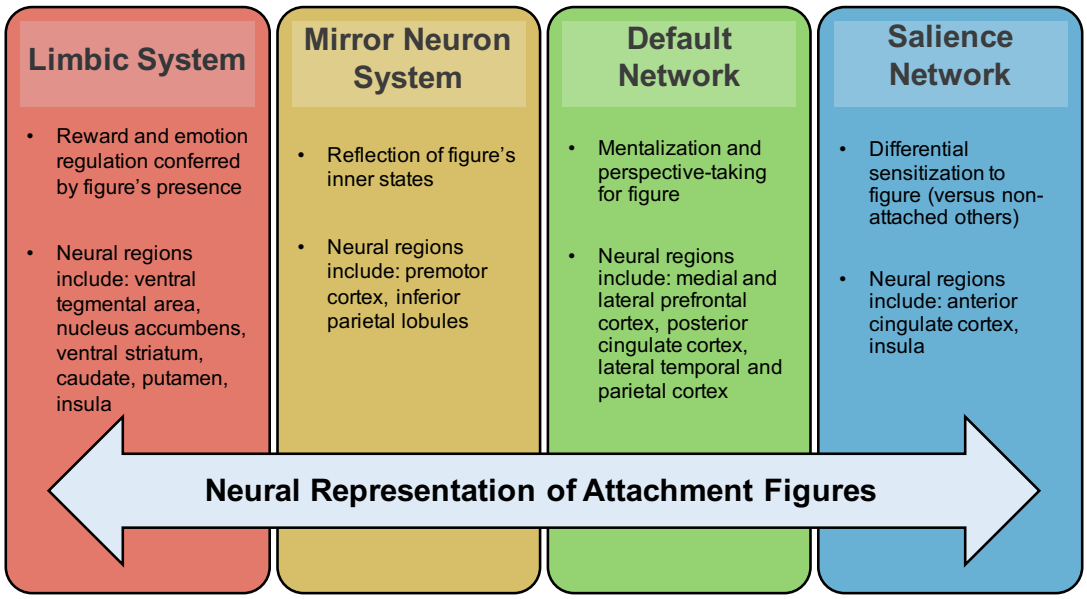

Figure 2.1. Integrated model of the neural regions and networks recruited in representing attachment figures

This integrative model (Figure 2.1) is supported not only by the individual contributions of each of the task-based fMRI studies discussed in this section but also by recent resting state functional connectivity analyses of "in love" participants (Song et al., 2015). Being deeply "in love" may be associated with changes in the functional architecture of the brain, specifically measured by increased functional connectivity within a network of regions important for reward, motivation, and emotion regulation (including the dorsal ACC, caudate, NAcc, and insula) and,

separately, within another network of "social cognition" regions resembling the canonical default network (including the PCC, mPFC, precuneus, temporo-parietal junction, and inferior parietal lobe) (Song et al., 2015). Our synthesis shows the interplay between cortical and subcortical regions of the brain, all necessary and each playing different roles to support distinct facets of our complex representations of close others. To be able to draw meaningful conclusions from these findings, however, it is important to refer back to their methodological discrepancies.

Methodological Differences Characterize Existing Research

In the next section of this review, we employ a different approach towards integrating this literature. Here, we look across recent fMRI studies of close other mental representations with respect to their methods. Of particular interest to us are experimental parameters reflecting how researchers measure "closeness" when studying neural responses to social cognitive stimuli. Here, we discuss the: usage of terminology relating to close relationships; collection of relationship length data; self-report measures of closeness with relationship partners; social cognitive tasks used in the MRI scanner; and specific condition contrasts used in blood oxygen level dependent (BOLD) fMRI data analysis. We also track sample sizes, as well as gender, sexual orientation, and age composition of these studies' samples.

Terminology

Even a cursory glance at the terminology used by existing studies provides some rationale for their diverse findings. Authors use varied, but specific, language to operationally define their constructs of interest. They often continue to use this language in reporting and promoting research findings in their articles. Of the studies we surveyed, a majority describe their construct of interest as "romantic love" (e.g., Acevedo et al., 2012; Aron et al., 2005; Inagaki & Eisenberger, 2011; Langeslag et al., 2014). Other studies focus on "close others" or

"close relationships" (e.g., Heatherton et al., 2006; Krienen, Tu, & Buckner, 2010), "familiar others" (e.g., Beckes, Coan, & Hasselmo, 2013), "attachment figures" (e.g., Eisenberger et al., 2011; Laurita, Hazan, & Spreng, 2017), or "significant others" (e.g., Tacikowski et al., 2011). These discrepancies in terminology preclude meaningful integration of findings across concepts and fields. With various studies employing vastly different—and, at times, ambiguous—terminology, we cannot assume that these studies assess one consistent construct of close other neural representations.

Relationship length

Relationship length is an essential descriptive statistic in such investigations. A social relationship is comprised of countless salient memories amassed over its course – whether that is a few weeks or numerous years. We assume that close other neural representations would not be identical across differing relationship timepoints. Relationship length is also meaningfully related to the measurement of attachment; while infatuation peaks within the first year of a romantic relationship, behavioral features (e.g. safe haven and secure base) indicating that a full-fledged attachment bond has formed may not be completely present until two years or more into the relationship (Hazan & Shaver, 1987). Accurately portraying relationship length plays a critical role in informing the relationship between behavioral shifts over the timecourse of a relationship and neural representation changes.

Yet, the existing literature reveals a lack of reported relationship length data. Half of the studies reviewed do not report any relationship length descriptive statistics for the target close relationships. For those who do report this variable, average (arithmetic mean) length of relationships with target relationship partner range from a few months (Langeslag et al., 2014, <9 months; Stoessel et al., 2011, <6 months; Younger et al., 2010, <9 months) to many years

(Acevedo et al., 2012, 21 years; Petrican, Rosenbaum, & Grady, 2015, 40.17 years). Several studies list a minimum or maximum relationship length as participation criteria but do not report average relationship lengths. Still more studies do provide descriptive statistics of their samples' relationship duration. Lastly, the terminology used to describe relationship length often does not capture the nuances inherent to this variable. For example, not all authors distinguished between how long ago participants may have starting dating or married versus first met their current relationship partners. Although longitudinal research that compares neural activation patterns at different relationship timepoints is minimal, the existing work does show notable trends in the recruitment of neural regions and networks related to relationship length (Xu et al., 2011; Xu et al., 2012). Current fMRI research does not recruit or report on a wide-enough range of participant relationship lengths to capture a full understanding of how this variable relates to other neural and behavioral outcome variables.

Self-report measures of "closeness"

Relationship length data alone, while important to characterize the expected relationship status represented by a sample of participants, is not sufficient to characterize an individual's feelings of closeness or attachment with his or her partner. It is necessary to include self-report measures to capture participants' emotions and thoughts regarding their relationships. Collecting these data helps provide an accurate sense of what participants' social neural representations may indicate. Just under half of the studies we reviewed do not describe any specific self-report measures used to assess relationship closeness or quality. Most who have administered self-report closeness measures rely heavily on the Passionate Love Scale (PLS) (Hatfield & Sprecher, 1986). Many studies that include a relationship closeness self-report measure administered only the PLS. The PLS assesses cognitive, emotional, and behavioral components of passionate love.

The Likert-type items on this scale probe for partner preoccupation, idealization, physical attraction, and desire (Hatfield & Sprecher, 1986). The PLS is not an ideal proxy for relationship closeness, as it focuses entirely on participants' feelings of infatuation or passionate love. In fact, PLS items more closely represent the documented "symptoms" of infatuation (Tennov, 1979) than a durable pair bond. Additionally, asking participants to complete only the PLS about their romantic partner could lead to priming neural responses with cues of high reward and approach motivation.

A few studies (e.g., Acevedo et al., 2012; Beckes, Coan, & Hasselmo, 2013; Laurita, Hazan, & Spreng, 2017) utilize the Inclusion of Other in the Self (IOS) scale (Aron, Aron, & Smollan, 1992). The IOS is a single-item pictorial measure of closeness and interconnectedness in dyads. The seven instances of two overlapping circles of the IOS range from mutually exclusive to highly overlapping in appearance (Aron, Aron, & Smollan, 1992). The IOS is a direct self-report measure of perceived closeness with relationship partners, as it is a visual representation of how individuals think of their partners and themselves. Yet, there is little space for objective clarification of responses to the IOS. It is possible to view the highly overlapping circles as a negative, enmeshed state not representative of an ideal close relationship.

One study (Acevedo et al., 2012), utilizes the PLS, the IOS, the Eros subscale of the Love Attitudes Scale (LAS) (Hendrick & Hendrick, 1986), and the Friendship-Based Love Scale (FBLS) (Grote & Frieze, 1994). The FBLS is intended to measure comfortable, affectionate, trusting love for a likable partner, based on a deep sense of friendship. The FBLS is a nine-item Likert-type measure (Grote & Frieze, 1994). While the FBLS is a well-suited complement to the PLS, it does not measure all the components of closeness on its own. The Eros subscale of the LAS assesses levels of passionate love—initial attraction and perceived "chemistry" for

instance—in one's relationship with a romantic partner (Hendrick & Hendrick, 1986). In our own recent study (Laurita, Hazan, & Spreng, 2017), we took a similar approach to Acevedo and colleagues (2012) in collecting self-report data, as we administered a comprehensive relationship battery (see Appendix 2.A).

Many studies implement other measures related to relationship closeness or to different relationship quality factors such as satisfaction. Of the studies that do administer other self-report closeness measures, only a few report the resulting behavioral data (e.g., Beckes, Coan, & Hasselmo, 2013; Laurita, Hazan, & Spreng, 2017) or utilize participants' responses as variables in their neuroimaging analyses (e.g., Acevedo et al., 2012). The inconsistencies in usage of self-report closeness measures restrict our ability to make conclusive statements about close other representations in the brain. Collectively, we have not defined what is meant by "close" with respect to social relationship representations.

Social cognitive tasks used in the MRI scanner

There was also great variety seen in the tasks used to evoke neural representations of close others. Most of the studies we examined implement an experimental paradigm in which participants view facial images of their target relationship partner(s) versus control images (e.g., Acevedo, 2012; Inagaki et al., 2016; Scheele et al., 2013; Zeki & Romaya, 2010). Within this category, there are several variations on the social cognitive task used, including unpleasant heat stimulations paired with the various facial images (Eisenberger et al., 2011), one-back repetition tests (Gobbini et al., 2004), and oddball tasks with photos as targets or distractors (Langeslag et al., 2014). Beyond facial image viewing, other tasks include trait judgment of partner versus others (Heatherton et al., 2006; Krienen, Tu, & Buckner, 2010; Laurita, Hazan, & Spreng, 2017; Wang et al., 2012), and support giving or receiving from partner versus others (Coan, Schaefer,

& Davidson, 2006; Inagaki & Eisenberger, 2011). One study used the administration of oxytocin to participants as an independent variable in their experiment (Scheele et al., 2013). Another recent study does not include a specific social cognitive task but instead looks at how romantic love may be associated with neural functional architecture, by assessing functional connectivity in a resting state scan for "in love" participants (Song et al., 2015).

It is probable that the diverse social cognitive tasks we choose lead to distinct patterns of activation in the brain. For instance, we would expect to see different findings in response to a partner trait-judgement task (e.g. Krienen, Tu, & Buckner, 2010) versus a partner hand-holding experimental paradigm (Beckes, Coan, & Hasselmo, 2013). Although these tasks may be assessing the same construct of cognitive representations of close relationships, the relevant representations are likely activated for distinct motivational purposes across the studies mentioned above.

Specific condition contrasts used in BOLD fMRI data analysis

Each of the studies in the above section includes control conditions for activation contrasts within their BOLD fMRI data. Most studies use exclusively social contrast conditions such as a less-close friend, a highly familiar other, an acquaintance, a known famous figure, or a complete stranger. Others include non-social controls—such as the categorization of a typographical font (Wang et al., 2012). When studying social closeness, it is crucial to control for as many other interpersonal factors as possible. For instance, including conditions for a familiar but non-close other or a friend known for an equal amount of years as a romantic partner would allow for better isolation of the social closeness variable.

Scheele and colleagues (2013) demonstrate the importance of including a variety of social contrasts, introducing famous-other and then familiar-other faces as a specific controls to

romantic partners faces in their discovery and replication studies, respectively. This methodological choice allowed them to interpret their activational results as specific to close others—not simply familiar others. In our aforementioned study (Laurita, Hazan, & Spreng, 2017), we also examine close other representations using several relevant social condition contrasts. By including a variety of social contrast conditions in our study, we were able to isolate patterns of neural activity specific to primary attachment figure representations. However, it is increasingly clear that few neuroimaging studies have systematically assessed the continuum of personal relatedness and attachment in this way.

Size and demographic composition of samples

Samples range from 10 (Gobbini et al., 2004) to 98 (Krienen, Tu, & Buckner, 2010) subjects scanned. Several studies only scanned heterosexual females as part of partner-pairs (e.g., Coan, Schaefer, & Davidson, 2006; Petrican, Rosenbaum, & Grady, 2015), and one study included only heterosexual males in romantic relationships (Scheele et al., 2013). Most studies include primarily college-aged, young adults, with only a few examining older adults (Acevedo et al., 2012; Petrican, Rosenbaum, & Grady, 2015). These inconsistencies and shortcomings in study demographics further cloud our understanding of neural representations of close others. It is clear that we need to direct attention and resources towards studying men, non-exclusively-heterosexual individuals, and older adults. The close relationships literature is rife with gender differences, and there is substantial reason to believe that neural representations of close others may be different across genders (e.g., Burleson, 2003; Diamond, 2003; Hendrick & Hendrick, 1995). Most of the existing literature on sex differences focuses on differences in attachment styles. For example, Del Guidice conducted a meta-analysis in 2011, finding that males show higher avoidance and lower anxiety in attachment than do females. Zeki and Romaya (2010)

found no gender or sexual orientation differences in brain activation. Yet, undiscovered differences could certainly exist

Recommendations, and a Proposal for a Standardized Assessment Battery

Although we are far from achieving the goal of cohesive integration of cognitive and social theories of relationships, we can progress toward consistent utilization of theoretically- and empirically- based methodological procedures and increased awareness of attachment theory's applications. Here, we offer a series of recommendations (see Table 2.1) designed to promote an interdisciplinary approach for mapping the neural representation of our closest relationships, conceptualized as attachment bonds:

1) Increased awareness of attachment theory as a guiding framework through cross-disciplinary collaborations

In this review, we discuss the applicability of adult attachment theory to the study of neural representations of close others. Since attachment bonds in adulthood are quantifiable and their associated behaviors, emotions, and cognitions are already well-studied, we believe this to be a fruitful approach to categorizing our closest social relationships. Only once relationships are adequately described and categorized can we expect to find reliable patterns of neural activity that reliably underlie their representations.

Until recent years, there has been only minimal evidence of cross-talk between social-psychological theorists and social-cognitive neuroscientists regarding the study of close relationship representations. Despite significant overlap in researchers' topics and populations of interest, few examples of collaborative projects exist, to date (e.g., Acevedo et al., 2012; Eisenberger et al., 2011; Laurita, Hazan, & Spreng, 2017). As part of this recommendation, we hope to promote cross-disciplinary collaborations that bring together experts from these fields.

We believe that such partnerships would enable the effective application of attachment theory and would yield clearer neuroimaging results.

2) More focused participant recruitment to capture the full spectrum of social relationships

In human subjects research, it is often difficult to fully control for pre-existing characteristics that may be related to study outcomes. Yet, it is necessary that we do what we can to improve construct validity and reliability. We should recognize the connection between accurate self-report of data describing participants' close relationships and how we eventually characterize a representative sample. One way to move towards greater consistency within a sample and generalizability to other samples would be to include relationship criteria as part of more focused recruitment strategies. For example, researchers could recruit participants who maintain attachment relationships with a romantic partner and/or a parent (according to self-report and/or relationship length data).

3) Design of neuroimaging tasks that directly capture how participants behaviorally utilize attachment figure mental representations

A study's motivations are inherently connected to its results through the careful design of its experimental paradigm. As evidenced by the variety of fMRI tasks we cover in the present review, there is space for both replications and constructions of different tasks in future research. We argue that the design of neuroimaging tasks can be better-informed by understanding the affective, behavioral, and cognitive processes involved in representing close others. We recommend that researchers explore different types of tasks that require active mentalization about or utilization of attachment figure representations. Passive tasks will not require participants to draw upon their attachment figure representations in replicable or consistent ways. Examples of active mentalization tasks include, but are not limited to, trait judgement, or social

autobiographical memory, accompanied by target name or photograph prompts that are individualized for each participant. Other rigorous designs that would require utilization of attachment figure representations include real or simulated presence of attachment figures in threat-induction paradigms (e.g., hand-holding task).

4) Necessary inclusion of social controls in neuroimaging tasks

We believe this point is important enough to be a separate recommendation; it is challenging to draw conclusions about any close other neural representations if social contrasts are not intentionally included. Implications of task-based fMRI findings rely on our ability to compare patterns of activation across different conditions. We recommend that all studies of close other representations include targets such as romantic partners, family members, close friends, acquaintances, famous figures, strangers, and the self as control conditions that are social in nature and possess ecological validity. Within the broad social category of known others, there may be substantial differences along the dimensions of closeness and familiarity. To parse out behavioral and neural differences between several known others, studies could require participants to think of specific exemplars of each of these dimensions: an attached romantic partner or family member, a friend with whom the participant is close and familiar but not attached, a familiar but not close acquaintance, and a known but not close or familiar famous figure. Ideally, future fMRI studies will capture patterns of brain activity for more complete spectra of familiarity and closeness.

5) Implementation of rigorous methodological practices needed for statistical power in neuroimaging studies, including larger sample size and proper reporting of brain and behavioral data

Increased interest in neural correlates of social psychological constructs must go hand-in-hand with adherence to rigorous methodological practices needed for neuroimaging studies (for review, see Button et al., 2013; Mar, Spreng, & DeYoung, 2013; Poldrack et al., 2017; Yarkoni, 2009). It is not reasonable to interpret individual differences in a sample of thirty fMRI participants or to draw any conclusions from a sample of ten; such investigations can actively muddle this emerging field of close relationship neuroscience. Likewise, minimal inclusion of behavioral data reflects an inadequate understanding of the overlap between psychology and neuroscience in understanding close relationships. Both brain data and behavioral data should be collected and reported in accordance with the highest standards of both disciplines.

6) Utilization of a standardized battery of self-report measures

Importantly, we need to administer self-report measures that answer numerous questions about participants' cognitions, behaviors, and emotions within the context of their relationships. Some of the questions we would certainly want future participants to answer include: To whom are participants attached? How do participants view their social closeness with specific others? Toward whom do participants feel passionate love? Toward whom do participants feel companionate love? What attachment style do participants show in their current romantic relationships? How committed, satisfied, and invested do participants feel in their current romantic relationships? How long have participants been in relationships with their romantic partners? How long have participants known specific other people?

Answers to these questions could let us know, on a basic level, the core drivers of regional and network brain activation differences. If we implement a standard battery of measures addressing these and other questions across studies, we can begin to tap into a unified cognitive construct of attachment figure mental representations. Such a standard battery can

provide a clear picture of the content of attachment figure mental representations, the attachment "status" and style, and the specific ways in which attachment figure representations are different from other social representations.

Our proposed standard battery can be found in Appendix 2.A. This compilation of close relationship self-report measures includes the WHOTO (Fraley & Davis, 1997; Hazan et al., 1991), IOS (Aron, Aron, & Smollan, 1992), PLS (Hatfield & Sprecher, 1986), FBLS (Grote & Frieze, 1994), ECR-R-PS (Fraley, Waller, and Brennan, 2000), and brief partner-specific and general relationship questionnaires of our own design. Each measure serves a specific purpose in providing clear, attachment-related information about an adult's close relationships. The WHOTO (Fraley & Davis, 1997; Hazan et al., 1991) is an attachment functions measure that determines the people with whom subjects display attachment relationships. The items are based on four attachment-related components: proximity seeking, separation distress, safe haven, and secure. Subjects list up to four most important figures in their lives by generic labels (e.g. "mother", "husband") for each of the ten items. The Partner-Specific Experiences in Close Relationships Scale (ECR-R-PS) (Fraley, Waller, and Brennan, 2000), is a measure designed to assess individual differences with respect to attachment-related anxiety and avoidance. This partner-specific version assesses these differences within the context of subjects' current romantic relationships. Responses to ten items are on a seven-point Likert scale.

Lastly, we include brief questionnaires in order to gain consistent self-report data about variables such as relationship length. The partner specific items assess commitment, exclusivity, and satisfaction, whereas the general questions gauge depth of personal knowledge and emotional investment in any kind of relationship. By including each of these measures, in addition to the highly relevant IOS (Aron, Aron, & Smollan, 1992) and complementary PLS

(Hatfield & Sprecher, 1986) and FBLS (Grote & Frieze, 1994), we account for whom participants feel the closest to and what their attachment status is. Completion of this battery provides extensive information about participants' potential attachments to romantic partners, in particular.

Concluding Remarks

Various regions of the brain, including those important for reward, emotional regulation, memory, and understanding of others' actions, are recruited in the activation of mental representations of attachment figures. The neural systems involved in the formation and function of mental representations in adult attachment relationships are understandably complex. In the present work, we call attention to an emerging field of close relationship neuroscience and a gap in its literature that would benefit greatly from increasing collaborations across disciplines.

We have asserted that the developing social neuroscience of attachment is based in a rich theoretical framework. Attachment theory suggests that behavior towards certain close others differs fundamentally from behavior towards more distant others. One important characteristic of attachment bonds is the feeling of security associated with attachment figures' proximity. As individuals undergo conditioning processes over the course of relationship development, the accessibility of attachment figure mental representations supplants the need for physical proximity. Social cognitive neuroimaging studies implicate a wide array of brain systems in supporting attachment figure representations. Engagement of reward systems, as well as the distress-alleviation mechanism within the limbic system, have been implicated in attachment formation and maintenance. Past work also highlights the role of the limbic system in emotional regulation provided by a close other. Memory systems support the encoding and retrieval of person-specific knowledge and social memories necessary to form rich cognitive representations.

The default network has also been implicated in differentiating mental representations of oneself and of known others. Lastly, the salience network demonstrates a critical ability to distinguish primary attachment figure representations from other social representations. Past studies have, however, applied diverse approaches to operationalize and measure the constructs of close relationship representations or attachment figure representations.

In light of the excitement and confusion surrounding this new area of research, we have offered a series of recommendations designed to promote an interdisciplinary approach for mapping the neural basis of attachment figure representations. We assert that administration of standardized assessments, including measures of attachment status, style and relationship quality, is necessary to develop comprehensive, reliable and replicable markers of real-world attachment representations. In addition to uniting the contributing neuroimaging fields, future research could include implementation of longitudinal designs investigating which neural structures are sensitive to the affective, behavioral, cognitive, and physiological processes involved in attachment figure mental representations. In the future, it could be possible to learn how neural representations of primary attachment figures within a romantic couple or a parent/adult child relationship change over the course of a lifetime spent together. We might also be able to examine what kinds of interpersonal experiences, specifically, recruit neural regions of interest within the context of close other mental representations. We already have evidence for how crucial attachment bonds are for our psychological and physical health throughout the life course; with cross-disciplinary communication and sharing of methodological tools, the possibilities to learn more about the brain's function in these powerful relationships are limitless.

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Table 2.1. Recommendations to Promote an Interdisciplinary Approach to Close Relationship Neuroscience

Our Recommendation	One Example of Implementation
1. Increased awareness of attachment theory as a guiding framework through cross-disciplinary collaborations	Initiate research partnership between social psychologist and cognitive neuroscientist
2. More focused participant recruitment to capture the full spectrum of social relationships	Recruit participants who, based on self-report data, maintain attachment relationships with a romantic partner and/or a parent
3. Design of neuroimaging tasks that directly capture how participants behaviorally utilize attachment figure mental representations	Utilize a social-cognitive task that requires active mentalization, such as trait judgment
4. Necessary inclusion of social controls in neuroimaging tasks	Include targets of romantic partners, family members, close friends, acquaintances, famous figures, strangers, and self as control conditions
5. Implementation of rigorous methodological practices needed for statistical power in neuroimaging studies, including larger sample size and proper reporting of brain and behavioral data	Collect and report descriptive statistics for all self-report data pertaining to relationships
6. Utilization of a standardized battery of self-report measures	Include measures found in Appendix 2.A

CHAPTER 3

Dissociable patterns of brain activity for mentalizing about known others: A role for attachment

We continually update our representations of other individuals and utilize those representations, especially about persons with whom we form attachment relationships, to guide social behaviors. The hallmarks of these unique, close social bonds are feelings of security and concomitant affect-regulatory benefits associated with attachment figures' presence (Bowlby, 1982; Mikulincer & Shaver, 2007a; Sroufe & Waters, 1977). In infant development, attachment is theorized to play a pivotal role in maintaining proximity to the primary caregiver (Bowlby et al., 1982). Lack of perceived proximity, and accompanying distress, engages attachment representations. These attachment representations in turn provide comfort and security, facilitating exploration, in a constantly shifting system of behavioral dynamics. The extension of this theoretical framework, to explain adult romantic relationships (Hazan & Shaver, 1987), currently serves as a predominant paradigm for understanding the regulatory powers of close social bonds (Hazan, Gur-Yaish, & Campa, 2004; Pietromonaco, Feldman Barrett, & Powers, 2006). The so-called "chronic accessibility" (Andersen, et al. 1990; Baldwin et al., 1993) of attachment figure mental representations comes about due to learning and conditioning under this inborn system of attachment bonding that is operative across the lifespan.

Recent research demonstrates that attachment figure mental representations serve various functions contributing to health and happiness. Just bringing to mind the cognitive representation of one's romantic partner, for example, promotes recovery following recollection of upsetting autobiographical memories (Selcuk, et al., 2012), provides distress alleviation when giving a public speech (Grewen, et al., 2003), decreases the neural response to threat with partner

hand-holding (Coan, et al. 2006), and reduces the subjective experience of pain (Eisenberger et al., 2011). Importantly, evidence supports the notion that these mental representations are flexible; shifts in cognition, behavior, and patterns of neural activation can be associated with changes in attachment.

Recent neuroimaging results show the involvement of many brain regions, and associated brain networks, in creating, updating, and using mental representations of close others. Several studies highlight the role of the dopaminergic reward system, particularly of areas such as the mid-insula, anterior cingulate cortex (ACC), caudate head, ventral tegmental area (VTA), and putamen, in motivating pair bond formation and maintenance and in the regulation of emotion associated with thinking of a close other (Acevedo et al., 2012; Bartels & Zeki, 2000; Stoessel et al., 2011; Younger et al., 2010; Zeki & Romaya, 2010; see Feldman, 2016 for review). Research utilizing threat-anticipation tasks also links the emotion-regulatory capabilities of close other mental representations with various limbic system regions (Coan, Schafer and Davidson, 2006).

Others associate activation of regions within the default network, a functionally-connected assembly of brain regions broadly implicated in internally-directed cognition, with mental representation of social others. Core brain areas within the default network include medial and lateral temporal lobes, medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), and lateral parietal cortices (Andrews-Hanna, Smallwood & Spreng, 2014). The default network is associated with several aspects of social cognition, including mentalizing (or, making inferences about other people's mental states) (Andrews-Hanna et al., 2014). Personal experiences are thought to be an important mechanism in the generation of social conceptual knowledge which, in turn, leads to development and implementation of strategic social behavior (Spreng and Mar, 2012).

Neuroimaging research commonly uses trait-judgment paradigms to assess cognition related to social others. Early work by Mitchell, Macrae, and Banaji (2006) demonstrated the role of the mPFC in differentiating similar versus dissimilar other representations. With respect to studies of close-other cognitive representations, neural regions of interest include the mPFC and PCC (e.g., Gobbini et al., 2004; Heatherton et al., 2006; Krienen, Tu, & Buckner, 2010; Platek et al., 2006; Tacikowski et al. 2012, 2013; Wang, et al., 2012). Within the literature on mentalizing, studies focus on the role of the default network in differentiating close others from strangers or self. Personal judgments about friends, over and above those about strangers, engage a network of brain regions in mPFC, PCC/retrosplenial cortex, inferior parietal lobe, lateral temporal cortex, and medial temporal lobe (Krienen, Tu, & Buckner, 2010). Recruitment of these regions for friend judgments suggests that the default network plays a role in formation or access of representations of known others. Further, representations of the self are associated with greater engagement of mPFC, over and above representations of intimately known others (Heatherton et al., 2006), suggesting that social proximity or attachment modulates engagement of this region, and the default network more broadly. However, no single study investigates the full spectrum of social proximity.

Here we use fMRI to examine the neural representation of known others along a continuum of attachment. We use a trait-judgment task, requiring participants to make personal judgments about a romantic partner, parent, close friend, familiar acquaintance, and the self. Our goal was to determine how mental representations of salient attachment figures and others in our social world are associated with patterns of brain activity, and whether these patterns are modulated by the presence of a primary attachment bond. We predicted that, overall, trait judgments about all known people and the self, relative to a matched control condition, would

engage mPFC and PCC. This hypothesis is consistent with literature investigating mentalizing and the default network (Mar, 2011; Andrews-Hanna, Smallwood & Spreng, 2014). We also predicted that neural representations of self and attached romantic partners would be differentiable from representations of parents and friends. Strong evidence exists for the differential behavioral, physiological, cognitive, and emotional responses to attachment figures—and, particularly, primary attachment figures—versus less close others (Hazan, Gur-Yaish, & Campa, 2004). As romantic partner representations are more salient than other social representations (e.g. Aron et al., 1991; Pietromonaco, DeBuse, & Powers, 2013), we hypothesized that judgments for self and romantic partners would share a common pattern of brain activity encompassing the salience network, a collection of brain regions implicated in the detection and processing of salient environmental stimuli (Uddin et al., 2015).

Materials and Methods

Participants

Participants were 29 healthy, right-handed young adults (16 females, 13 males; *M* age = 24 years, *SD* = 3.5 years) with normal or corrected-to-normal visual acuity, and no history of psychiatric, neurological, or other medical illness that could compromise cognitive functions. Participants gave written informed consent in accordance with the Institutional Review Board of Cornell University. Participants were selected for the scanning procedure based on the study criteria of being in a long-term, committed, exclusive romantic relationship.

Assessment of attachment

We recruited participants on the basis of romantic relationship length and characteristics, asking that participants be in an exclusive and committed relationship for around two years or longer. Two years is an important milestone within adult attachment theory, as it is the time

around which full-fledged attachment bonds have formed (Hazan & Shaver, 1987). The average participant relationship length (measured in months) was well above twenty-four (M=39.55 months, SD= 17.13).

Participants completed a pre-scan survey about their various personal relationships. Participants first provided one name per relationship condition in response to prompts (see Appendix 3.A). This survey included self-report measures of attachment (WHOTO; Fraley & Davis, 1997; Hazan et al., 1991), perceived closeness (Inclusion of Other in Self, IOS; Aron, Aron, & Smollan, 1992), and relationship length. Additionally, the survey included the Experiences in Close Relationships – Revised Partner Specific (Fraley, Waller, & Brennan, 2000), Friendship-Based Love Scale (Grote & Frieze, 1994), Passionate Love Scale (Hatfield & Sprecher, 1986), and a partner-specific questionnaire designed to assess relationship quality factors, such as satisfaction, commitment, exclusivity, and emotional investment (see Appendix 3.A). We confirmed participants' attachment relationships and subsequent inclusion in the study based on these self-report variables.

The WHOTO (Fraley & Davis, 1997; Hazan et al., 1991) is an attachment functions measure that determines the people with whom subjects display attachment relationships. Items are based on four attachment features: proximity seeking, separation distress, safe haven, and secure base. Subjects list up to four most important figures in their lives for each of the ten items. The WHOTO can be used in various ways to measure individuals' attachment to others. In the present study, we used the WHOTO in two distinct ways. First, we utilized it as a continuous measure of attachment with romantic partners, parent, and friends by scoring each item based on the individual's ranking (highest scores = listed first) and totaling these scores; therefore higher WHOTO total scores were indicative of greater levels of attachment. Second, we examined the

presence of primary attachments to either romantic partner or parent by scoring each item on a binary of "[partner/parent] listed first?" = 1 and "[partner/parent] *not* listed first?" = 0.

We also investigated social cognitive closeness using the IOS scale (Aron, Aron, & Smollan, 1992). This scale is a single-item pictorial measure of closeness and interconnectedness in dyads. The seven instances of two overlapping circles of the IOS range from mutually exclusive to highly overlapping in appearance. The IOS is a direct self-report measure of perceived closeness with relationship partners, as it is a visual representation of how individuals think of others and themselves.

Task and fMRI Design

During fMRI scanning, we used a trait-judgment task (c.f. Grigg & Grady, 2010) in which participants were asked to think about several people in their lives mentioned by name in the pre-scan survey. Each trial contained a trait adjective and a person's name; participants rated the person on each trait adjective, on a scale of 1 (unlike this person) to 3 (very much like this person). Blocks were composed of 5 trials in which participants were instructed to hold the person in mind continuously while making each trait judgment about that person. Blocks were interleaved with 10 seconds of fixation. We also included a motor control condition block, in which participants were prompted with "Which number?", shown a number 1, 2, or 3, and instructed to respond by pushing the button corresponding to that number.

The experiment consisted of 350 trials divided across 5 runs, each consisting of 14 blocks, in turn comprising 5 trials per block. Trials were 3-seconds long, and a 1-second crosshair fixation screen appeared between each trial. There were 2 blocks per run for each of the 7 conditions (partner, parent, close friend, familiar acquaintance, famous person, self and "which number" motor control). See Figure 3.1 for behavioral paradigm. The order of conditions within

each run was randomized. Each task run lasted 7 minutes and 40 seconds. The 5 runs were then counterbalanced for each participant to eliminate any possibility of ordering effects of the fixed condition order and adjective order.

Numerous participants reported uncertainty in performing this task for the famous person condition, and the neural results were a multivariate outlier. For these reasons, the famous person condition was excluded from subsequent analyses and interpretation.

Figure 3.1.

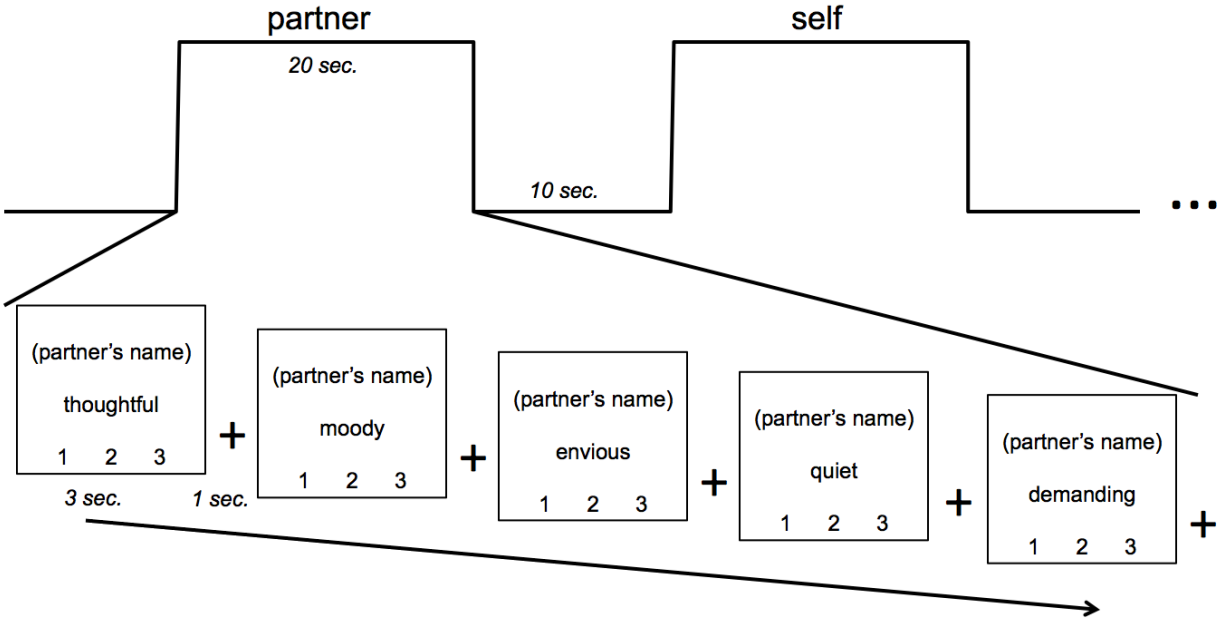

Figure 3.1. Behavioral paradigm, involving trait-judgment task for social others

50 trait adjectives were selected for the study in order to ensure that each word was used exactly once for each condition. The trait adjectives were selected from a list of popularly used personality terms (Anderson, 1968). The trait adjectives were presented in a fixed order across blocks, such that each trait adjective was paired exactly once with each condition.

Magnetic Resonance Image Acquisition

Brain imaging data were acquired using a 3T GE Discovery MR750 MRI scanner with a 32-channel head coil. This MRI scanner was located within the Cornell Magnetic Resonance Imaging Facility in Ithaca, New York. Anatomical scans were acquired using a T1-weighted volumetric MRI magnetization prepared rapid gradient echo (TR = 7.7 ms; TE = 3.4 ms; 7° flip angle; 1.0 mm voxels with no gap, 176 slices). Five 7 m 40 s experimental runs of blood–oxygen level dependent (BOLD) functional scans were acquired with a T2*- weighted multi-echo imaging pulse sequence (TR = 2000 ms; TEs = 12.7, 27.5, and 43 ms; 77° flip angle; 33 axial slices; matrix size = 64 x 64; field of view (FOV) = 240 mm; 33 axial slices; 3.8 mm thick slices).

Preprocessing of Magnetic Resonance Imaging Data

BOLD fMRI data were preprocessed to correct for motion, physiological noise and scanner artifacts using Multi-Echo Independent Components Analysis (ME-ICA) with meica.py (Kundu et al., 2012). ME-ICA is a method for de-noising fMRI data based on information about the T2* decay of the BOLD signal, acquired through multi-echo fMRI. Using ME-ICA, multi-echo fMRI datasets can be decomposed into independent components before these components are categorized as BOLD or noise/non-BOLD. ME-ICA robustly de-noises fMRI data by removing all non-BOLD components (Kundu et al., 2012; Lombardo et al., 2016). Within the ME-ICA program, the BOLD fMRI images were also normalized, spatially, to the standard space of the MNI template. Subsequently, data were resampled to 2x2x2-voxel volumetric time-series and smoothed with a 6-mm full width half maximum (FWHM) Gaussian kernel.

fMRI Analysis

Partial Least Squares

Task-based analyses were performed using the multivariate technique partial least squares (PLS), a multivariate functional neuroimaging analysis technique used to identify whole-

brain patterns of activity that are correlated with tasks (Krishnan, Williams, McIntosh, & Abdi, 2011; McIntosh, Chau, & Protzner, 2004). PLS identifies a set of orthogonal latent variables (LVs) that optimally relate BOLD signal and the experimental design. The statistical significance of the detected patterns is assessed through permutation testing, whereas reliability is determined in an independent step by iterative bootstrap resampling with replacement.

PLS is sensitive to a distributed voxel response, rather than the activity of individual voxels per se, and assesses the covariance between brain voxels (BOLD signal) and the experimental design to identify a limited number of orthogonal components (LVs) that optimally relate the two. This data-driven approach determines orthogonal whole-brain patterns of activity that covary with the experimental design. Within the PLS framework, brain activity is constrained to examine the covariance between brain activity and task design. In this regard, we are able to examine robust patterns of activity only associated with the experimental conditions. Along these same lines, PLS is capable of analyzing multiple conditions simultaneously to examine covariance of response across conditions. The current study design was optimized for a PLS analysis to assess distributed patterns of activity across conditions.

Activity for each voxel was averaged across blocks for each relationship condition and normalized relative to activity at fixation preceding the trait judgment. The data matrix was expressed as a voxel-by-voxel deviation from the grand mean across the entire experiment, which was decomposed using singular value decomposition to derive the LVs representing task contrasts. Each brain voxel is given a singular value weight, known as a salience (akin to a component loading in principle component analysis), which is proportional to the covariance of voxel activity with the task contrast represented by each LV. Multiplying the salience by the BOLD signal value in that voxel and summing the product across all voxels gives a composite

brain activity score for each participant on a given LV. We then used these brain scores to examine similarities and differences in brain activity across conditions and across participants. Greater activity in brain areas with positive (or negative) weights on a specific LV yields positive (or negative) mean brain scores for a given condition. PLS results can be interpreted as identifying co-varying sets of brain regions in which activity is reliably associated with the specific condition-wise contrasts represented by each LV.

The significance of each LV was determined by permutation testing, using 500 permutations with random reordering of the task conditions for each participant. PLS is recalculated for each permutation sample, and the frequency in which the permuted singular value exceeds the observed singular values is determined and expressed as a probability. In a second, independent, step the reliability of the saliences for the brain voxels across participants, characterizing each pattern identified by an LV, was determined by bootstrap resampling with replacement, using 100 iterations, to estimate the standard errors for each voxel. We set a minimum bootstrap ratio (conceptually similar to a Z-score) at 2.58 equivalent to $p < 0.01$. Because the analysis is performed across voxels in a single step, no correction for multiple comparisons is required.

Systematic region of interest (ROI) analyses were conducted for several seed regions within mPFC, utilizing 9 peak coordinates from a recent parcellation of this region (de la Vega et al., 2016). ROIs were extracted from the following areas and corresponding MNI coordinates: supplementary motor area (SMA; 0, -14, 54), pre-supplementary motor area (pre-SMA; 0, 4, 62), posterior dorsal midcingulate cortex (pdMCC; 0, 12, 50), anterior dorsal midcingulate cortex (adMCC, 0, 28, 48), posterior ventral midcingulate cortex (pvMCC; 0, -2, 30), anterior ventral midcingulate cortex (avMCC; 0, 36, 24), dorsal medial prefrontal cortex (dmPFC; 0, 50, 28),

pregenual anterior cingulate cortex (pgACC; 0, 46, 8), and ventral medial prefrontal cortex (vmPFC; 0, 48, -12). Using PLS, we performed a multiple-voxel extraction with a neighborhood size of 1 for each of these coordinates. This analytic approach yielded mean response intensities, averaged across subjects, for each condition. Each region was submitted to a simple t-test to evaluate activation against baseline. We report on this analysis for each of the 9 ROIs.

Results

Behavioral Results; Assessment of Attachment

Our first analyses examined two critical measures: reported attachment status (WHOTO) and closeness (IOS) between romantic partners, parents, and friends. Descriptive statistics for these measures are in Table 3.1. We initially conducted repeated measures ANOVA tests across WHOTO total scores and across IOS scores. Results showed a significant difference between means of romantic partner, parent, and friend WHOTO scores ($F(2, 56) = 22.14$, $p < 0.001$). Results of non-parametric analyses mirrored these ANOVA results, as a Friedman test yielded significant differences among repeated measures $\chi 2$ $(2, N = 29) = 40.55$, $p < 0.001$. We conducted this non-parametric test to account for alternative perspectives that consider WHOTO scores as ordinal data. Results also showed a significant difference between means of romantic partner, parent, and friend IOS scores ($F(2, 56) = 68.00$, $p < 0.001$).

We ran several post-hoc t-tests to clarify the nature of attachment-related differences between specific comparison groups of interest. Results showed that participants reported significantly greater attachment to romantic partners over parents ($t_{(56)} = 5.22$ $p < 0.001$) and closeness with partners over parents ($t_{(56)} = 5.52$, $p < 0.001$). Participants also reported significantly greater attachment to romantic partners over friends ($t_{(56)} = 13.69$, $p < 0.001$) and closeness with partners over friends ($t_{(56)} = 5.08$, $p < 0.001$). Lastly, participants reported

significantly greater attachment to parents over friends ($t_{(56)} = 7.28$, $p < 0.001$), but there was no difference in reported closeness between parents and friends ($t_{(56)} = -0.09$, $p = 0.92$). Taken together, these results demonstrate that participants' romantic partners and parents were attachment figures—with participants showing more attachment to partners than parents—whereas friends were, on average, not attachment figures for the participants. Our general categorization of friends as non-attachment figures is supported by previous theoretical work and behavioral results suggesting young adults' relationships with friends do not show characteristic features of attachment bonds (Hazan & Zeifman, 1994; Fraley & Davis, 1997).

Importantly, we further utilized participants' WHOTO data to determine their primary attachment figures. Most participants listed their romantic partners first across several WHOTO items. This distinction was especially pronounced for the WHOTO items reflecting proximity seeking, separation distress, and safe haven, whereas participants listed parents and partners first at about equal rates for secure base; this finding reflections past observations about the transition of primary attachment figures from parents to partners in early adulthood, with secure base often the final feature to be primarily directed towards partners (Hazan & Zeifman, 1999; Nickerson & Nagle, 2005). Overall, these results provide strong evidence that romantic partners served as participants' primary attachment figures, whereas parents did not.

Neuroimaging Results

The PLS analysis focused on investigating neural activity changes across relationship conditions (partner, parent, friend, acquaintance, self, and control). PLS analyses revealed two significant patterns of activity.

The first significant LV separated all social other- representations from the control (i.e. number matching) condition. This result replicates previous findings implicating the default

network in mentalizing about others (Mar, 2011; Krienen, Tu, & Buckner, 2010). Significant activations for this LV were found within areas of dorsomedial prefrontal cortex (dmPFC), ventromedial prefrontal cortex (vmPFC), and PCC. Other significant activations for this LV were observed in occipital cortex, inferior frontal gyrus, temporal pole, thalamus, superior temporal sulcus, cerebellum, anterior temporal lobe, caudate head, middle cingulate gyrus, basal ganglia, precentral gyrus, and intracalcarine cortex (Figure 3.2, Table 3.2).

Figure 3.2.

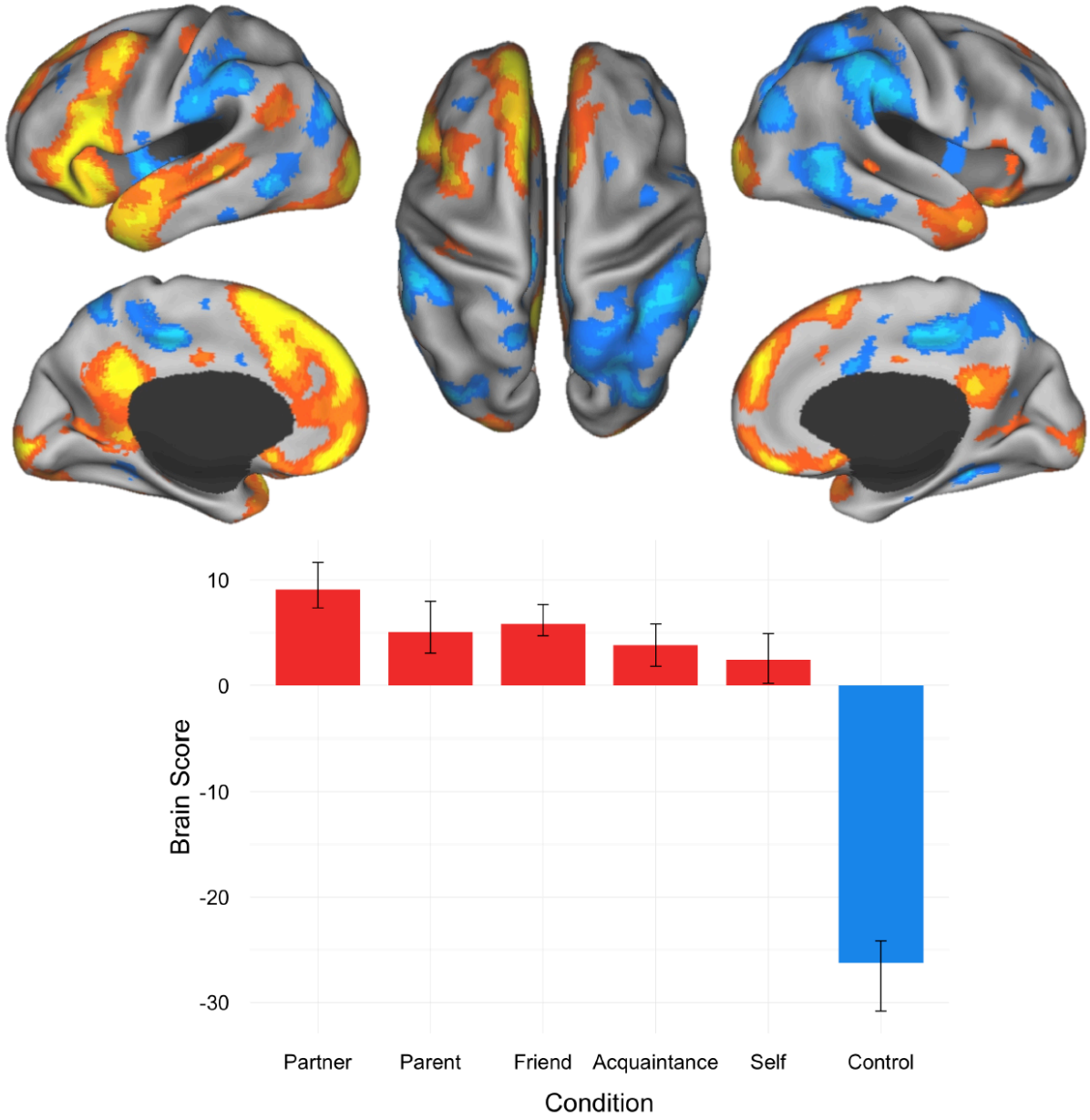

Figure 3.2. Results of the task PLS analysis contrasting activity across partner, parent, close friend, familiar acquaintance, self, and control conditions; LV1 Activation map & brain scores with 95% confidence intervals. Brain scores represent cross product of the group result image and the individual subject BOLD response for each given LV. Warm colors on activation maps (red, orange, yellow) correspond to positive brain scores, shown by red plotted bars. Cool colors on activation maps (shades of blue) correspond to negative brain scores, shown by the blue plotted bars. (*Left*) Lateral and medial views of left hemisphere. (*Center*) Dorsal view. (*Right*) Lateral and medial views of right hemisphere.

A second significant LV was observed, central to our hypothesis regarding differentiation of attached romantic partner representations versus parent and friend representations. This LV dissociated brain activity for partner and self from parent and friend. Anterior insula, anterior and middle cingulate, and posterior superior temporal sulcus (STS) were associated with partner and self representations. Activations in frontal gyrus, occipital fusiform gyrus, cerebellum, precuneus, frontal pole, supramarginal gyrus, anterior superior frontal sulcus, occipital cortex, thalamus, precentral gyrus, posterior dmPFC were also associated with partner and self representations. In contrast, parent and friend judgments engaged left temporal pole and parahippocampal gyrus. Acquaintance and motor control conditions did not contribute to the multivariate pattern (Figure 3.3, Table 3.3).

Figure 3.3.

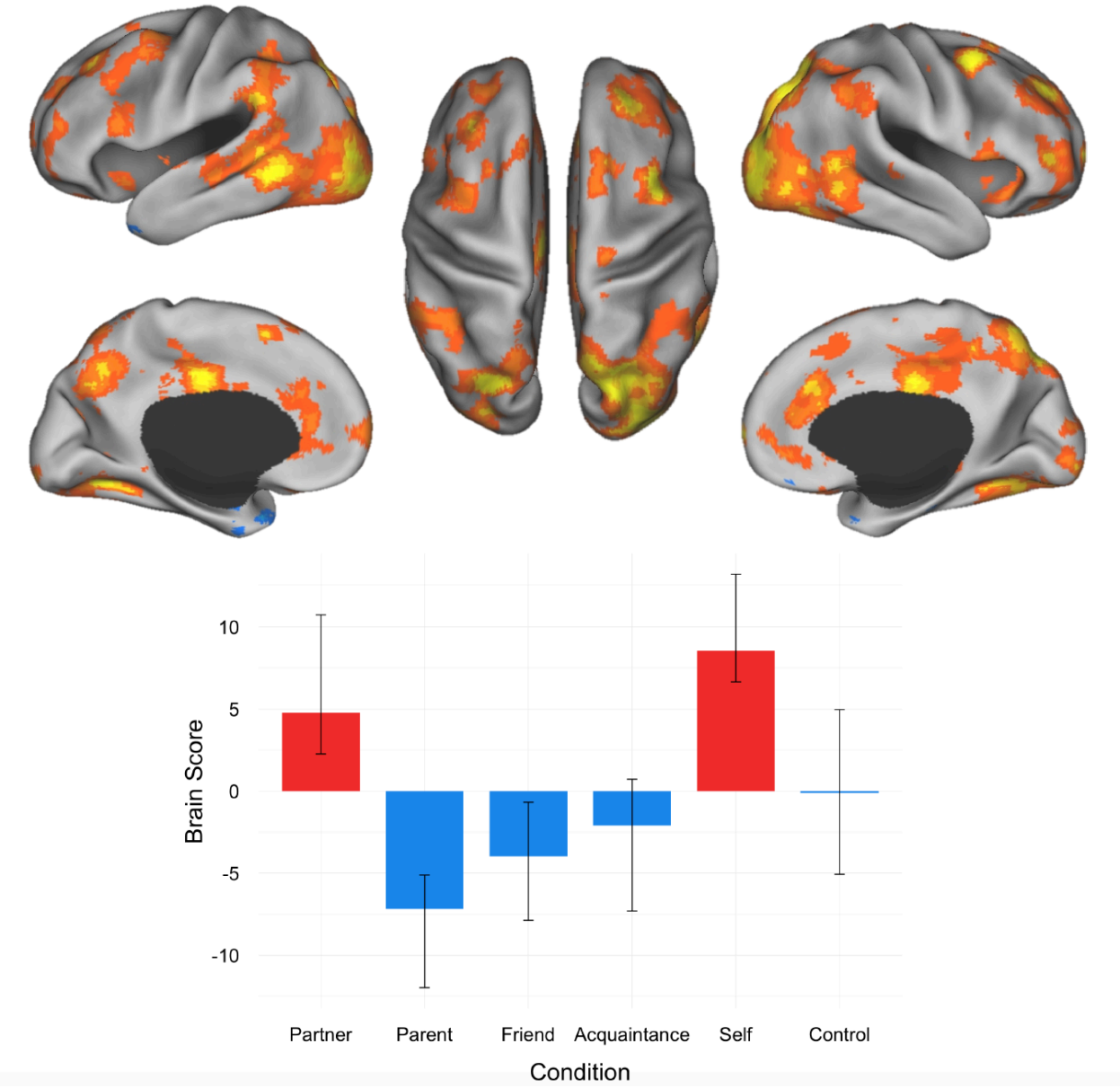

Figure 3.3. Results of the task PLS analysis contrasting activity across partner, parent, close friend, familiar acquaintance, self, and control conditions; LV2 Activation map & Brain scores with 95% confidence intervals. Brain scores represent cross product of the group result image and the individual subject BOLD response for each given LV. Warm colors on activation maps (red, orange, yellow) correspond to positive brain scores, shown by red plotted bars. Cool colors on activation maps (shades of blue) correspond to negative brain scores, shown by the blue plotted bars. (*Left*) Lateral and medial views of left hemisphere. (*Center*) Dorsal view. (*Right*) Lateral and medial views of right hemisphere.

For our ROI analyses, we conducted simple t-tests ($\alpha = 0.05$) comparing each condition's voxel intensity response against baseline. Distinct patterns of response were observed for specific areas within mPFC. Most notably, results showed significant positive activation intensity for dmPFC and adMCC across all of the social cognitions (partner, parent, friend, acquaintance, and self). This pattern was similar for vmPFC, with partner, parent, and friend showing significant positive intensities, avMCC, with partner, friend, acquaintance, and self showing significant positive intensities, and pgACC, with partner and self showing significant positive intensities (Figure 3.4).

Figure 3.4.

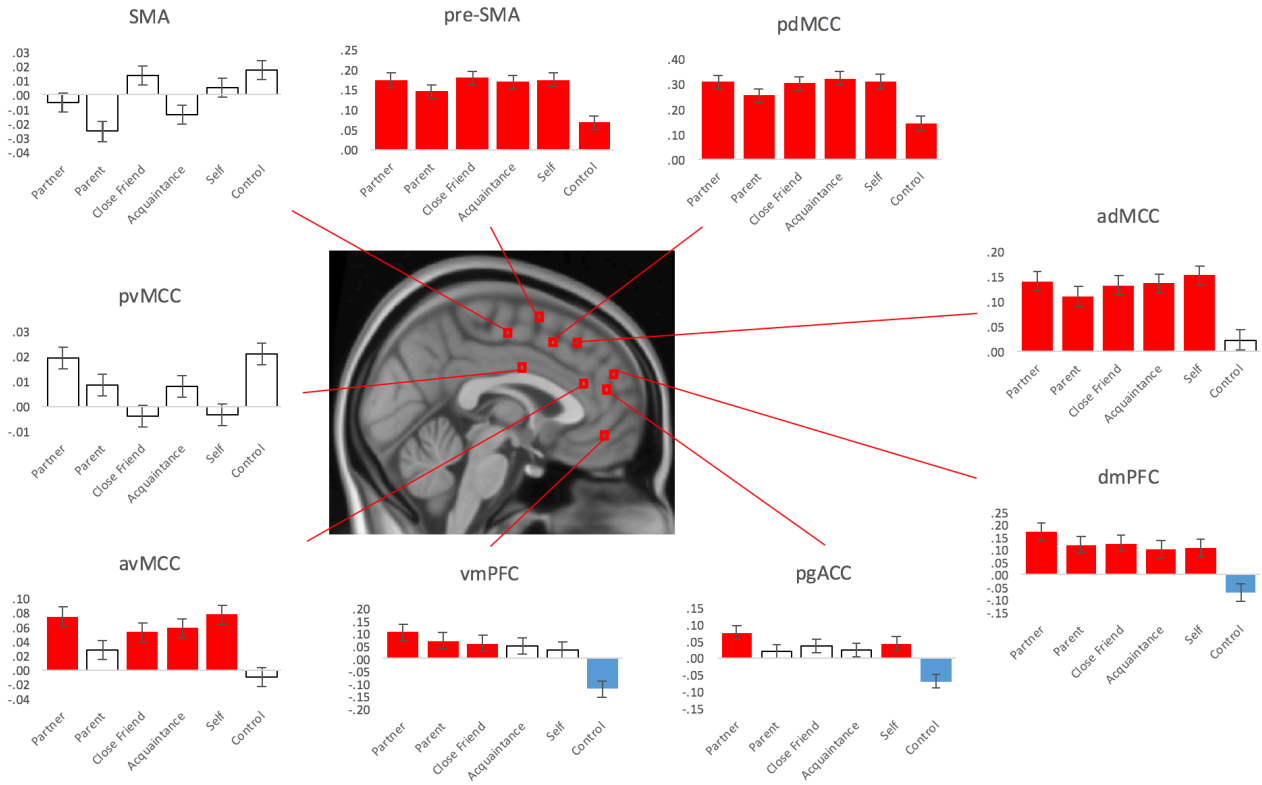

Figure 3.4. Results of ROI analysis examining 9 seed regions within mPFC. Significance is shown through the different colors within the bar graphs; red plotted bars correspond with significant positive response intensities, blue plotted bars correspond with significant negative response intensities, and clear plotted bars correspond with non-significance.

Discussion

The present study aimed to determine how mental representations of other individuals in our social world reflect underlying patterns of neural activity and, more specifically, how our brains represent others with whom we share attachment bonds. First, we successfully replicated findings on mentalizing (Heatherton et al. 2006; Krienen, Tu, & Buckner, 2010; Mar, 2011), as all social conditions and the self condition engaged regions of the default network including dmPFC, vmPFC, and PCC, in addition to lateral PFC. Second, our results showed that presence of a primary attachment bond modulated neural activation associated with the mental representation of others. Specifically, anterior cingulate cortex, anterior insula, and posterior STS were associated with representations of attached romantic partner and self versus less-close others. Lastly, our ROI analysis results highlighted the role of vmPFC and dmPFC in representing social others and the self, with rostral cingulum regions showing robust activation for romantic partner.

In line with our predictions, results replicated the role of the default network in social cognitive processing, including mentalizing (Andrews-Hanna et al., 2014; Mar, 2011). Increased activation within dmPFC, vmPFC, PCC was associated with all of the conditions involving mentalizing, a critical component of social cognition (Mar, 2011), versus the control condition. Default network brain regions have been associated with attributional decisions, judgments of others' emotional states (Haas, Anderson, & Filkowski, 2015), and imagining the experiences of others (Hassabis et al., 2014; Krienen, Tu, & Buckner, 2010). Activations outside the default network were also observed. Recruitment of lateral PFC has been observed in studies of social cognitive reasoning (Mar, 2011), consistent with the role of maintaining social information online (McKinnon & Moscovitch, 2007). The left lateralization is also consistent with verbally

mediated processes (Nagel et al., 2013). Activity in thalamus, basal ganglia, and caudate could indicate recruitment of the limbic system for emotional regulation in response to social cues (Coan, Schafer, & Davidson, 2006). Occipital cortex activity, often related to visual object recognition (Malach et al., 1995), was possibly recruited in imagining images of social others.

A second significant pattern dissociated brain activity for judgments about partner and self from parent and friend. Increased activation in anterior cingulate, anterior insula and posterior STS was observed in mentalizing about partner and self. These regions have been implicated in social cognitive processes crucial for close bond formation, such as empathy (Decety & Jackson, 2006). The pattern of brain activity associated with partner and self judgment is consistent with the topology of the salience network (Seeley et al., 2006). The salience network, including regions such as anterior insula and anterior cingulate, is thought to coordinate responses to environmental stimuli that are most important to an individual (see Uddin, 2015, for review), such as representations of primary attachment figures and self, suggesting that this network may differentiate representations of self and romantic partners serving as primary attachment figures from other social representations. These results demonstrate that nuanced differences between neural representations of salient social figures (partner, parent, friend, and self) are likely associated with differences in attachment status. Engagement of the salience network dichotomized our attachment schema, showing greater activation during mentalizing about one's self or a romantic partner versus one's parent or a friend.

Contrary to previous work suggesting the default and salience networks work in opposition (Hermans et al., 2014), we found these networks are recruited together to represent romantic partners and the self. The antagonistic relationship observed between these networks in

past research may have more to do with the tasks used, which do not assess personal significance as we do in the present work. Our results confirm these networks work in concert, similar to research showing both competition and interdependence between default network function and salience network integrity (Bonelle et al., 2012). Research in moral cognition also suggests an interactive role for these two networks (Sevinc & Spreng, under review). Salience network regions such as anterior insula detect both internal and external salient events, interacting with the default network to process internal events specifically. We observed this interaction in the unique neural response to attached romantic partners and the self, wherein the default network is engaged in construction and utilization of social representations and the salience network is selectively attuned to the most meaningful of these representations.

Since cognitive representations of attachment figures are chronically accessible and serve emotion-regulatory functions, they are understood to be different in content and use from representations of less-close others (Mikulincer & Shaver, 2007a; Pietromonaco, Feldman Barrett, & Powers, 2006). The mental representations we form of close others are composed of perceptually salient social memories and, yet, are differentiable depending on the specific person about whom we are thinking. As a pair bond forms, a romantic partner becomes integrated into one's sense of self — into one's head (Aron et al., 1991) and "under [one's] skin" (Pietromonaco, DeBuse, & Powers, 2013). Recent work in neurobiology highlights biobehavioral synchrony as a characteristic of pair bonds (Feldman, 2016). In many cases, the presence of intrinsically rewarding contact comfort and sexual activity also enables romantic attachment relationships that are uniquely intimate in nature (Zayas, Merrill, & Hazan, 2015). Our finding that representations of romantic attachment partners and of the self have common neural underpinnings confirmed these theoretical principles.

In early development, parents serve as our primary attachment figures, a role often supplanted by romantic partners in young adulthood (Hazan & Zeifman, 1999; Nickerson & Nagle, 2005). Both our self-report and neuroimaging results note this social-psychological distinction; romantic partners were predominately nominated by participants as primary attachment figures. Furthermore, we observed that overall romantic partner attachment was higher than parent attachment, closeness to a parent as measured by the IOS was no different from closeness to a friend, and friend and parent brain activity covaried together. Our findings indicate that, although both romantic partners and parents categorically served as attachment figures for participants, there are subtle differences in attachment status across these categories—observable in both brain and behavior—that require further exploration. We assert these differences are related to the distinctive status of primary attachment figures and, relatedly, to the unique physical and emotional intimacy of romantic relationships. These differences could be better understood by asking participants additional questions about the nature of their romantic relationships, such as "Do you currently share a home with this person?".

Left temporal pole and parahippocampal gyrus showed increased activity for parent and friend over partner and self. Recent work suggests that parahippocampal regions play a critical role in judgments of trustworthiness and uncertainty (Bhatt et al., 2012). Parahippocampal involvement may reflect visual input related to the task or the retrieval of previous experiences with the person about whom the participant was making a judgment (Aminoff, Kveraga, & Bar, 2013). The temporal pole is thought to integrate social conceptual knowledge, enabling processes like empathy (Pehrs et al., 2015) and sharing others' embarrassment (Müller-Pinzler; Paulus et al., 2014). Within the context of our experimental paradigm, these neural regions may uniquely contribute to trait judgment for these individuals of varied closeness. These activity patterns

could be associated with differences in cognitive processing necessary to access more distal social conceptual knowledge for others who are close to us but not primary attachment figures, for whom judgments are more readily retrieved.

Results of our ROI analyses confirmed the role played by dorsal and ventral areas of mPFC in social cognition. We found activity in dmPFC and vmPFC was robustly associated with thinking about all social others and the self. Our results support the functional separation noted in de la Vega and colleagues' (2016) tripartite mPFC parcellation. These subregions fall within the "anterior zone" and, in the present study, also fit within the functional profile of this zone, important for social cognition, affect, decision making, and episodic memory (de la Vega et al., 2016). We note, consistent with the second latent variable, that rostral cingulum regions demonstrated a robust response to romantic partner.

Overall, these findings enhance our understanding of neural representations of known others and how attachment modulates these representations. As our experimental stimuli included names of real individuals, highly-relevant to each participant, our findings provide ecologically valid evidence that mentalizing about close others is associated with different patterns of brain activation depending on social proximity and attachment. Unlike previous studies, which involved more passive tasks (e.g. viewing photos of known others), our paradigm required active mentalizing about personalized, social targets. Our initial findings provided validation of this paradigm by replicating previous findings of default network activation associated with mentalizing about known others and provided the first evidence that this association is consistent across multiple levels of social closeness. The second pattern of activity provided unique insights with respect to modulation of these neural representations by attachment. The covariance of partner and self, showing activity within the salience network,

suggests that we form highly overlapping neural representations for ourselves and romantic attachment figures. Interpretation of our results provides a potential mechanistic explanation for the differentiated neural response to close others; while the default network more broadly supports social cognition for known others and the self, recruitment of the salience network is critical for capturing the nuanced representations, and their significance, of our most "intimate" adult relationships: romantic partners serving as primary attachment figures and the self.

Our findings provide empirical evidence to support recent work on the topic of attachment indicating that human attachment representations recruit cortical and subcortical networks for processes such as mentalization and reward (Feldman, 2016). Future work should further consider the role of attachment in dissociable patterns of brain activity. The neural correlates of relationship quality factors—specifically, attachment styles (e.g., secure, anxious, avoidant)—remain undiscovered. Further investigations could examine individual differences in attachment styles and neural foundations of mentalizing processes. In the current study, we leveraged valid and reliable self-report measures that reflect participants' potential attachments. Our set of measures provides extensive information about participants' thoughts, behaviors, and emotions within the context of their close relationships. For future studies involving known others, we recommend the administration of these measures as a standardized battery to assess the construct of adult attachment.

With this study, we introduce a common framework across disciplines to inform investigations of the neural basis of social attachment as a deeper view of social cognitive neuroscience. Attachment figure mental representations play a powerful role in assisting individuals with emotion regulation and navigation of their social environments. Further investigations could provide significant insight into how the brain represents attachment, perhaps

the most important consequence of real-world social interactions. Our findings support the hypothesis that mentalizing about different attachment figures – individuals from whom we seek proximity, security, and comfort – may engage unique brain response patterns. By utilizing adult attachment as one end of a spectrum of personal closeness, we can begin to disentangle some of the important functional areas and networks of the brain recruited in social cognition. Attachment styles and patterns of behavior are well-studied within social psychology; attachment theory may therefore provide neuroscientists with behavioral constructs at a high level of specificity with respect to social proximity. Here we provide preliminary support for the idea that, by utilizing attachment criteria, we can implement more directed empirical studies to differentiate how social relationships are represented in the brain.

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Table 3.1. Descriptive Statistics for Self-Report Measures

Measure	Romantic Partner	Parent	Close Friend	Acquaintance
WHOTO *(M, SD)* Out of 40	32.83, 6.80	22.31, 8.46	6.97, 7.56	-
IOS *(M, SD)* Out of 7	4.83, 1.23	2.93, 1.39	2.97, 1.55	1.55, 0.69
Relationship Length *(M, SD)* In months	39.55, 17.13	274.76, 57.76	83.52, 65.82	50.35, 48.12
"How well do you know this person?" *(M, SD)* Out of 5	4.79, 0.63	4.43, 0.98	4.31, 0.66	2.93, 0.88
"How familiar are you with this person?" *(M, SD)* Out of 5	4.79, 0.63	4.57, 0.95	4.45, 0.74	3.17, 1.00

Table 3.2. Peak Activation Coordinates, LV1

Region	Coordinates			BSR
	x	*y*	*z*	
Social > Control				
Medial Prefrontal Cortex	-10	58	30	-11.54
Dorsomedial Prefrontal Cortex	-8	20	56	-11.43
Occipital Cortex	-26	-94	4	-11.21
Inferior Frontal Gyrus	-58	24	14	-11.01
Posterior Cingulate Cortex	-8	-50	32	-10.75
Ventromedial Prefrontal Cortex	-4	54	-16	-9.52
Temporal Pole	-44	8	-38	-9.01
Occipital Cortex	18	-102	-10	-8.77
Inferior Frontal Gyrus	26	16	-22	-6.56
Thalamus	-8	-14	8	-6.50
Superior Temporal Sulcus	-54	-12	-8	-6.08
Cerebellum	4	-62	-40	-6.05
Anterior Temporal Lobe	62	0	-28	-6.04
Head of Caudate	-16	10	14	-5.64
Cerebellum	2	-58	-52	-4.81
Middle Cingulate Cortex	-2	-12	38	-4.66
Angular Gyrus	-50	-60	30	-4.64
Superior Temporal Sulcus	42	-34	0	-4.10
Pallidum/Basal Ganglia	-26	-8	-6	-3.77
Precentral Gyrus	-36	-20	52	-3.60
Intracalcarine Cortex	20	-66	6	-3.33
Control > Social				
Intraparietal sulcus	58	-44	46	10.47
Posterior Middle Cingulate	-12	-28	44	9.91
MT+	48	-54	4	8.48
Lateral Occipital Cortex	-42	-82	30	8.44
Intraparietal sulcus	-56	-36	52	8.43
MT+	-64	-62	-4	7.77
Mid- Insula	-44	-4	-2	7.16
SMA (Supplementary Motor Area)	-12	-10	62	6.81
Mid- Insula	38	-12	-6	6.21
Dorsal Anterior Cingulate	4	10	32	6.12
Thalamus	14	-30	2	5.59
Dorsolateral Prefrontal Cortex	44	40	0	5.41
Posterior Superior Frontal Gyrus	24	12	54	5.40

Dorsolateral Prefrontal Cortex	-32	32	38	5.34
Inferior Temporal Cortex	-62	-40	-26	5.33
Parahippocampus/Brain Stem	16	-16	-30	5.27
Dorsolateral Prefrontal Cortex	40	40	24	4.94
Lingual Gyrus	-32	-42	-8	4.81
Cerebellum	-38	-44	-46	4.75
Cerebellum	-16	-74	-48	4.54
Precentral Gyrus	38	-4	52	4.34
Posterior Superior Frontal Gyrus	-22	8	58	4.24
Frontal Pole	34	56	-16	3.84
Medial Orbital Sulcus	16	34	-20	3.64

Table 3.3. Peak Activation Coordinates, LV2

Region	Coordinates			BSR
	x	*y*	*z*	
Partner, Self > Parent, Friend, Acquaintance				
Middle Frontal Gyrus	40	10	56	6.99
Occipital Fusiform Gyrus	-28	-66	-2	6.64
Cerebellum	-42	-52	-40	6.34
Occipital Fusiform Gyrus	22	-84	-2	6.30
Dorsal Precuneus	16	-64	48	6.18
Dorsal Precuneus	-22	-76	50	6.06
Frontal Pole	16	68	2	6.06
Posterior Superior Temporal Sulcus	48	-52	4	5.60
Middle Cingulate Gyrus	-4	-18	36	5.50
Supramarginal Gyrus	-70	-42	30	5.15
Anterior Superior Frontal Sulcus	24	42	34	4.90
Anterior Cingulate Cortex	10	32	26	4.52
Occipital Cortex	-30	-100	18	4.47
Thalamus	22	-26	-2	4.34
Superior Frontal Gyrus	14	20	58	4.23
Precuneus	-10	-66	40	4.20
Ventral Anterior Cingulate Cortex	10	30	-8	4.20
Precentral Gyrus	-40	0	46	4.16
Cerebellum	-16	-60	-62	4.07
Anterior Superior Frontal Sulcus	-18	42	28	4.07
Cerebellum	-36	-90	-34	4.06
Cerebellum	-56	-66	-40	4.01
Posterior Dorsomedial Prefrontal Cortex	-10	12	56	3.95
Frontal Pole	42	46	0	3.89
Middle Frontal Gyrus	-32	30	40	3.88
Cerebellum	40	-60	-40	3.85
Superior Temporal Sulcus	-56	-22	-2	3.85
Frontal Pole	-20	70	4	3.82
Cerebellum	-46	-68	-56	3.68
Cerebellum	12	-54	-46	3.67
Rostral Anterior Cingulate	-4	40	10	3.67
Precuneus	6	-46	54	3.66
Inferior Frontal Gyrus	-60	20	14	3.51
Inferior Frontal Gyrus	52	16	2	3.43
Rostral Anterior Cingulate	0	48	-4	3.41

Inferior precentral sulcus	62	12	12	3.36
Superior Frontal Gyrus	-12	24	56	3.25
Anterior Insula	28	18	-10	3.23
Anterior Insula	-36	14	-12	3.07
Parent, Friend > Partner, Self				
Temporal Pole	-34	10	-34	-5.19
Parahippocampal Cortex	-24	-2	-42	-3.54

CHAPTER 4

Mentalizing about known others is associated with altered default network interactivity in older adulthood

Throughout the life course, we constantly form, update, and use cognitive representations of social others. Human social environments comprise complex hierarchies and feature wide spectra of relationships, ranging in proximity from close others and attachment figures to recently formed acquaintances. As close social relationships have been shown to confer various psychological and physiological benefits throughout the lifespan (Carstensen et al., 1996; Hoppmann & Gerstorf, 2009), it is perhaps one of our most crucial human cognitive capacities to be able to differentiate representations of close from less-close others in our social world.

Social cognition, and specifically our capacity to form and access representations of known others, has been associated with multiple brain systems. Social and evolutionary psychological theories have emphasized the highly-rewarding and functionally-adaptive nature of close social bonds, implicating the brain's reward and distress-alleviation systems (e.g., Acevedo et al., 2012; Bartels & Zeki, 2004; Coan, Schaefer, & Davidson, 2006). In contrast, cognitive psychological theories have focused on the specific processes through which representations of social others are formed, stored, and accessed, investigating how these processes and representations are implemented in the brain (e.g., Beckes, Coan, & Hasselmo, 2013; Heatherton, et al., 2006, Krienen, Tu, & Buckner, 2010). This latter line of research, emphasizing the processing of social representations, has implicated a number of brain areas in mentalizing, or attending to the mental state or characteristics of known others. These regions of the 'social brain' (Mitchell, 2008) closely overlap with the default network (DN), a functionally-

connected assembly of brain regions that has been associated with internal mentation and social cognitive processing (for review, see Spreng & Andrews-Hanna, 2015).

The default network is composed of areas along the cortical midline, including dorsal medial prefrontal cortex (dmPFC), ventral medial prefrontal cortex (vmPFC), and posterior cingulate cortex (PCC), as well as medial and lateral temporal cortices, lateral parietal lobes, and caudal portions of the lateral prefrontal cortex (Buckner et al., 2008; Andrews-Hanna et al., 2007). Together, these regions have been implicated in our ability to imagine the experiences of others (Hassabis et al., 2014; Spreng, Mar, & Kim, 2009), attribute and judge emotional states (Haas, Anderson, & Filkowski, 2015), reflect on beliefs (Young, Dodell-Feder, & Saxe, 2010), and form social impressions of known others (Cassidy & Gutchess, 2012).

Social representations may be stratified along multiple dimensions, including personal similarity (Mitchell et al., 2006), relational hierarchy (Tavares et al., 2015), and social proximity or 'closeness' (Krienen, Tu, & Buckner, 2010). Recent evidence suggests that these various dimensions of social-relatedness differentially impact how representations of social others are implemented in the brain (Thornton and Mitchell, 2017). In this context, social proximity (or closeness) in particular has been strongly implicated in the differential recruitment of the default network during social-cognitive tasks (Krienen et al., 2010; Gobbini, Leibenluft, Santiago & Haxby, 2004). Further, there is evidence that interactivity between default brain regions and other neural networks may be critical in the stratification of one's social world. For example, interactions between the default network and the medial temporal lobe memory system have been shown to support navigation of, or tracking shifting dynamics in and responding to, interpersonal relationships based on social affiliation and power hierarchies (Tavares et al., 2015). Similarly, we have recently shown interactions between the default network and brain regions

implicated in detecting personally salient stimuli (i.e. salience network, Uddin, 2015) during trait judgments of oneself and romantic partners but not for more socially distant others (Laurita, Hazan, & Spreng, 2017).

While much of the existing research investigating neural representations of social others has relied on young adult cohorts, few studies have examined this in older adults (e.g. Ebner et al., 2011; Ebner et al., 2013). Various social-cognitive abilities change across the adult lifespan, with evidence of both gains and losses (see Ebner et al., 2016 for a recent review). Within the domain of mentalizing about social others, the evidence for age-related change is somewhat equivocal. In a recent neuroimaging investigation, older adults performed more poorly than young on assessments of moral judgment and false-beliefs (Moran, Jolly, and Mitchell, 2012). In contrast, Castelli and colleagues (2010) reported equivalent performance for older and younger adults on a theory of mind task. As mentalizing about social others may depend on fluid intellectual or executive control processes (e.g. German and Hehman, 2006; Charlton et al., 2009), age-related declines in cognitive control may contribute to reduced social cognition in later life, although this idea remains controversial (Maylor, Moulson, Muncer & Taylor, 2002; Sullivan and Ruffman, 2004).

At the level of the brain, regions implicated in social functioning closely overlap with the default network (Mitchell, 2008). The default network undergoes significant change in normal aging, with evidence of reduced within network and increased between network connectivity (see Damoiseaux et al., 2017 for a review). It seems plausible then that these age-related changes may be associated with differences in mentalizing abilities between older and younger adults. Only a few studies have investigated this possibility directly. Moran and colleagues (2012) reported that activity in a core node of the default network, dmPFC, was reduced in older versus

younger adults during a series of social-cognitive tasks involving inferences about the intent, actions, and mental states of others. In another investigation, activity in dmPFC as well as other core default network nodes, including vmPFC and PCC, was reduced during negative (and increased during positive) impression formation in older versus younger adults (Cassidy, Leshikar, Shih, Aizenman & Gutchess, 2014). In contrast, an earlier study reported no age differences in activation or functional connectivity of the default network during a mentalizing task (Castelli et al., 2010). Interestingly, no performance differences were observed between the groups in this study, prompting the authors to speculate that greater recruitment of lateral PFC regions may have supported mentalizing ability in the older cohort.

Taken together, previous research suggests that for younger adults, the default network is implicated in social cognitive abilities, including mentalizing about social others. Further, the magnitude and topological pattern of default network engagement is modulated by social closeness. Despite well-documented changes in the default network with age, relatively little is known about how these changes impact mentalizing in older adulthood, and no studies have examined these changes across levels of closeness amongst known social others. Here we use fMRI to examine the neural representations of mentalizing about known others in young and older adults across a continuum of social closeness. Extending our recent study of young adults (Laurita et al., 2017), we used a trait-judgment task, to assess mentalizing, asking participants to make personal judgments about a romantic partner, a parent (young adults) or child (older adults), a close friend, a familiar acquaintance, and the self.

Consistent with previous works implicating the default network in mentalizing (Andrews-Hanna, Smallwood, & Spreng, 2014; Cassidy et al., 2014; Mar, 2011; Mitchell, 2008; Moran et al., 2012) we predict that both age-groups would engage core default network nodes while

making trait judgments about known others. Critically however, we expect age-differences to emerge in the modulation of default network interactivity across levels of social closeness. We have previously shown differential default network coupling with salience network brain regions during mentalizing about close from more distal social others (Laurita et al., 2017). However, a hallmark of neurocognitive aging is over-recruitment of lateral prefrontal brain regions during cognitive tasks (Grady, 2012), potentially reflecting greater reliance on control processes to support performance at lower levels of cognitive demand (Park and Reuter-Lorenz, 2009). Further, prefrontal and default network brain regions are functionally coupled and poorly modulated by task demand in older adults (Amodio & Frith, 2006; Heatherton et al., 2006; Rieck et al., 2017; Turner and Spreng, 2015). In the current study we predict that for older adults, default network engagement during the mentalizing task will show greater functional coupling with lateral prefrontal brain regions. In addition, default network interactions, as measured by connectivity with two heterogenous mPFC seeds (Denny et al., 2012; for review, see Wagner, Haxby, and Heatherton, 2012), will be less dynamic and poorly modulated by levels of social closeness during the mentalizing task.

Materials and Methods

Participants

Participants were 29 healthy, right-handed young adults (16 females, 13 males; *M* age = 24 years, *SD* = 3.5 years) and 27 healthy older adults (12 females, 15 males; *M* age = 67 years, *SD* = 6 years), with normal or corrected-to-normal visual acuity. All older adults scored over 26 on the Mini-Mental State Exam (MMSE; Folstein et al., 1975) and were not depressed, as measured by the Geriatric Depression Scale (GDS; Yesavage et al., 1983). Participants had no history of psychiatric, neurological, or other medical illness that could compromise cognitive

functions. In accordance with the Institutional Review Board of Cornell University, participants gave written informed consent prior to scanning. Across both age groups, study participants were selected for the scanning procedure based on the study criterion of being in a long-term, committed, exclusive romantic relationship. Results from the younger adults have been previously reported (Laurita et al., 2017).

Assessment of Self-Reported Closeness

Participants completed a pre-scan survey about their various personal relationships. Participants first provided one name per relationship condition in response to prompts (see Appendix 4.A). This survey included self-report measures of attachment (WHOTO; Fraley & Davis, 1997; Hazan et al., 1991) and perceived closeness (Inclusion of Other in Self, IOS; Aron, Aron, & Smollan, 1992). The WHOTO (Fraley & Davis, 1997; Hazan et al., 1991) is an attachment functions measure that determines the people with whom subjects display attachment relationships. Items are based on four attachment features: proximity seeking, separation distress, safe haven, and secure base. Subjects list up to four most important figures in their lives for each of the ten items. The WHOTO can be used in various ways to measure individuals' attachment to others. We utilized it as a continuous measure of attachment with romantic partners, parent, and friends by scoring each item based on the individual's ranking (highest scores = listed first) and totaling these scores; therefore higher WHOTO total scores were indicative of greater levels of attachment. We also investigated social cognitive closeness using the IOS scale (Aron, Aron, & Smollan, 1992). This scale is a single-item pictorial measure of closeness and interconnectedness in dyads. The seven instances of two overlapping circles of the IOS range from mutually exclusive to highly overlapping in appearance. The IOS is a direct self-report measure of

perceived closeness with relationship partners, as it is a visual representation of how individuals think of others and themselves.

Behavioral Task and fMRI Design

During fMRI scans, we used a trait-judgment task (c.f. Grigg & Grady, 2010; Laurita, Hazan, & Spreng, 2017). Participants were asked to think about several people in their lives mentioned by name in a pre-scan survey they completed. See Appendix 4.A for pre-scan prompts for each target person. Each trial contained a trait adjective and a target person's name; participants rated the target on each trait adjective, on a scale from 1 (unlike this person) to 3 (very much like this person). Blocks comprised 5 trials, all referring to the same person, in which participants were instructed to hold the target in mind continuously while making each trait judgment about that person. Blocks were interleaved with 10 seconds of fixation. A motor control condition block was included, in which participants were prompted with "Which number?", shown "1", "2", or "3" on the screen, and instructed to respond by pushing the button corresponding to that number. This particular control was chosen as it is a simple task for assessing baseline button-press response, it utilizes the same 3 buttons on the button box, it is non-social, in comparison to the other conditions, and it is consistent with prior block designs of mentalizing (e.g., Grigg & Grady, 2010), which allows for comparability between studies.

The experiment consisted of 5 runs, each consisting of 14 blocks with 5 trials per block; there were 350 trials in total. Trials were 3-seconds long, with a 1-second crosshair fixation screen separating each trial. There were 2 blocks per run for each of the 7 conditions: partner, parent (seen by young adults) or child (seen by older adults), close friend, familiar acquaintance, famous person, self, and "which number" control. The order of conditions within each run was randomized. Each task run lasted 7 minutes and 40 seconds. The 5 runs were then

counterbalanced for each participant to eliminate any possibility of ordering effects of the fixed condition order and adjective order. See Figure 4.1 for an example of this behavioral paradigm. The famous person condition was excluded from subsequent analyses and interpretation due to numerous participant reports of uncertainty in performing this portion of the task.

Fifty trait adjectives were selected for the study from a list of popularly used personality terms (Anderson, 1968). Adjectives were chosen at random but balanced for valence. See Appendix 4.B for list of adjectives. The trait adjectives were presented in a fixed order across blocks, such that each trait adjective was paired exactly once with each condition, or social other. Figure 4.1.

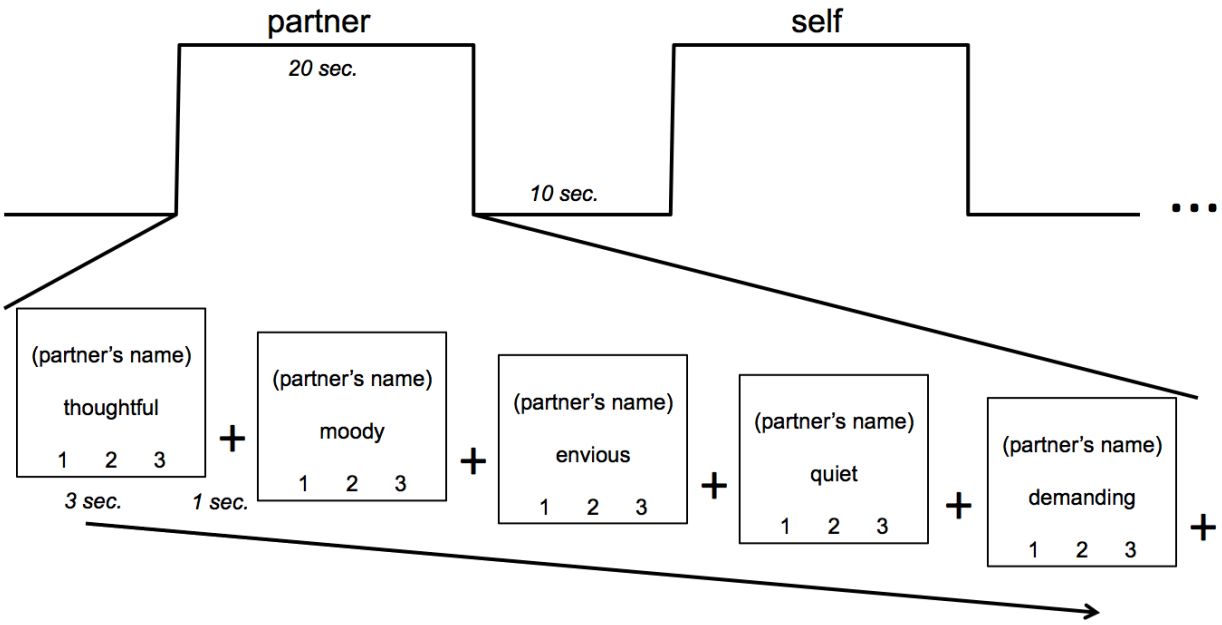

Figure 4.1. Behavioral paradigm, involving trait-judgment task for social others. Scale responses correspond to: 1 (unlike this person) to 3 (very much like this person).

Magnetic Resonance Image Acquisition and Preprocessing

Brain imaging data were acquired using a 3T GE Discovery MR750 MRI scanner with a 32-channel head coil. This MRI scanner was located within the Cornell Magnetic Resonance Imaging Facility in Ithaca, New York. Anatomical scans were acquired using a T1-weighted volumetric MRI magnetization prepared rapid gradient echo (TR = 7.7 ms; TE = 3.4 ms; 7° flip angle; 1.0 mm voxels with no gap, 176 slices). Five 7 m 40 s experimental runs of blood–oxygen level dependent (BOLD) functional scans were acquired with a T2*- weighted multi-echo imaging pulse sequence (TR = 2000 ms; TEs = 12.7, 27.5, and 43 ms; 77° flip angle; 33 axial slices; matrix size = 64 x 64; field of view (FOV) = 240 mm; 33 axial slices; 3.8 mm thick slices).

BOLD fMRI data were preprocessed to correct for motion, physiological noise, and scanner artifacts using Multi-Echo Independent Components Analysis (ME-ICA) with meica.py (Kundu et al., 2012). ME-ICA de-noises fMRI data based on information about the T2* decay of the BOLD signal, acquired through multi-echo fMRI. Using ME-ICA, the multi-echo fMRI datasets was decomposed into independent components before these components were categorized as BOLD or noise/non-BOLD. ME-ICA robustly de-noised the fMRI data by removing all non-BOLD components (see Kundu, 2017 for review; Kundu et al., 2012; Lombardo et al., 2016).

The BOLD fMRI images were normalized to a custom young-old population template derived from 50 younger (25 female; *M* = 22.02y, *SD* = 3.13y) and 50 older (25 female; *M* = 67.14y, *SD* = 6.7y) adults. Included template subjects were selected from an in-house brain bank for low trait motion, as recent work has indicated that trait motion can bias structural scans (mean FD = 0.09; Savalia et al., 2017). Anatomical images for included subjects were affine registered to MNI space using *@toMNI_Awarp* before being non-linearly, iteratively aligned

using *@toMNI_Qwarpar* in AFNI. Data were resampled to 2x2x2-voxel volumetric time-series and smoothed with an 8-mm full width half maximum (FWHM) Gaussian kernel.

Partial Least Squares fMRI Analysis

Task Activation

Task-based analyses were performed using the multivariate technique partial least squares (PLS), a multivariate functional neuroimaging analysis technique used to identify whole-brain patterns of activity or connectivity that are associated with tasks (Krishnan, Williams, McIntosh, & Abdi, 2011; McIntosh, Chau, & Protzner, 2004). PLS identifies a set of orthogonal latent variables (LVs) that optimally relate BOLD signal with the experimental design. The statistical significance of the detected brain response patterns is assessed through permutation testing, whereas reliability is determined in an independent step by iterative bootstrap resampling with replacement. Because these analyses are performed across voxels in a single step, no correction for multiple comparisons is required.

PLS is a data-driven approach that is sensitive to a distributed voxel response, rather than the activity of individual voxels per se, and assesses the covariance between brain voxels (BOLD signal) and the experimental design to identify a limited number of orthogonal components (LVs) that optimally relate brain voxels and experimental design. Using PLS, we were able to examine robust patterns of activity only associated with the experimental conditions. Along these same lines, PLS is capable of analyzing multiple conditions simultaneously to examine covariance of response across conditions. The current study design was optimized for a PLS analysis to assess distributed patterns of activity across conditions.

The mean centered PLS analysis was run in order to examine task-based activity across the whole brain. Activity for each voxel was averaged across blocks for each relationship

condition and normalized relative to activity at fixation preceding the trait judgment. The data matrix was expressed as a voxel-by-voxel deviation from the grand mean across the entire experiment, which was decomposed using singular value decomposition to derive the LVs representing task contrasts. Each brain voxel was given a singular value weight, known as a salience (akin to a component loading in principle component analysis), which is proportional to the covariance of voxel activity with the task contrast represented by each LV. Multiplying the salience by the BOLD signal value in that voxel and summing the product across all voxels gives a composite brain activity score for each participant on a given LV. We then used these brain scores to examine similarities and differences in brain activity across conditions and across participants. Greater activity in brain areas with positive (or negative) weights on a specific LV yields positive (or negative) mean brain scores for a given condition. PLS results can be interpreted as identifying co-varying sets of brain regions in which activity is reliably associated with the specific condition-wise contrasts represented by each LV.

Task-related Functional Connectivity

Task-related functional connectivity analyses were run in order to assess connectivity of mPFC, due to this region's known role in mediating social cognition (for review, see Spreng & Andrews-Hanna, 2015). These functional connectivity analyses were also performed using seed partial least squares (PLS; Krishnan et al., 2011; McIntosh, 1999). Seed PLS examines whole-brain functional activity that correlates with activity in a specified seed region. In seed PLS, LVs represent a decomposition of the covariance between activity in the seed and in all other brain voxels. Since the resultant LVs of seed PLS can identify multiple patterns of functional connectivity, this technique uniquely enables assessment of large-scale brain networks. In two-seed PLS analyses, activity was first extracted from regions of interest (including peak voxel in

the present dataset, and 26 neighboring voxels) in dmPFC and vmPFC (MNI coordinates: -6, 54, 30 and -2, 50, -18, respectively). This extracted activity was correlated across all other brain voxels and across all participants. PLS was then implemented to examine how patterns of correlation differed between conditions (i.e., romantic partner, parent/child, close friend, acquaintance, self, and control) and between young and older adults.

For the seed PLS analyses, the same set of resampling techniques were applied as described above for the task-based PLS. The significance of each LV was determined by permutation testing, using 500 permutations with random reordering of the task conditions for each participant. PLS is recalculated for each permutation sample, and the frequency in which the permuted singular value exceeds the observed singular values is determined and expressed as a probability. In a second, independent, step the reliability of the saliences for the brain voxels across participants, characterizing each pattern identified by an LV, was determined by bootstrap resampling with replacement, using 100 iterations, to estimate the standard errors for each voxel. We set a minimum bootstrap ratio (conceptually similar to a Z-score) at 2.58 equivalent to $p < 0.01$.

Results

Behavioral Results; Assessment of Closeness

Our first analyses examined two critical measures: reported attachment status (WHOTO) and closeness (IOS) between romantic partners, parents/children, and friends. Descriptive statistics for these measures can be found in Table 4.1.

We initially tested for interactions between condition (partner, parent/child, friend) and potential age effects, running an omnibus ANOVA test for WHOTO scores and another for IOS scores. There was a significant interaction between condition and age ($F(3, 52) = 3.28$, $p =$

0.028) for WHOTO scores. We further explored the effect of age in this interaction with post-hoc t-tests comparing young and older adults, within each condition. Older adults showed higher attachment as measured by the WHOTO to their partners than did young adults ($t(1, 54) = 4.68$, $p = 0.035$), whereas young adults showed higher attachment to their parents than older adults to their children ($t(1, 54) = 4.74$, $p = 0.034$). However, neither of these differences remained significant after correcting for multiple comparisons. No differences were observed between the age groups for friends $t(1, 54) = 1.60$, $p = 0.211$). Lastly, there was no significant interaction between condition and age ($F(3, 52) = 1.421$, $p = 0.25$) of closeness (IOS scores).

For the young adults alone, we then conducted repeated measures ANOVA tests across WHOTO total scores and across IOS scores. Results showed a significant difference between means of romantic partner, parent, and friend WHOTO scores ($F(2, 56) = 22.14$, $p < 0.001$). Results of non-parametric analyses mirrored these ANOVA results, as a Friedman test yielded significant differences among repeated measures $\chi 2$ (2, $N = 29$) = 40.55, $p < 0.001$. We conducted this non-parametric test to account for alternative perspectives that consider WHOTO scores as ordinal data. Results also showed a significant difference between means of romantic partner, parent, and friend IOS scores ($F(2, 56) = 68.00$, $p < 0.001$). For the older adults, we again conducted repeated measures ANOVA tests across these self-report scores. Results showed a significant difference between means of romantic partner, child, and friend WHOTO scores ($F(2, 52) = 127.96$, $p < 0.001$). Results of non-parametric analyses mirrored these ANOVA results, as a Friedman test yielded significant differences among repeated measures $\chi 2$ (2, $N = 27$) = 44.24, $p < 0.001$. Results also showed a significant difference between means of romantic partner, child, and friend IOS scores ($F(2, 52) = 28.17$, $p < 0.001$). Overall, these results

confirmed that the target individuals of partner, parent/child, and friend represented differing levels of perceived closeness and attachment, for both young and older adults.

Task Activation

In order to examine task-related activation, we ran a mean centered PLS analysis. This PLS analysis investigated differences in neural activity between young and older adults, and between all social-other conditions (partner, parent or child, friend, and acquaintance), the self, and the motor control condition. This task PLS analysis revealed two significant patterns of activity, or LVs.

Figure 4.2.

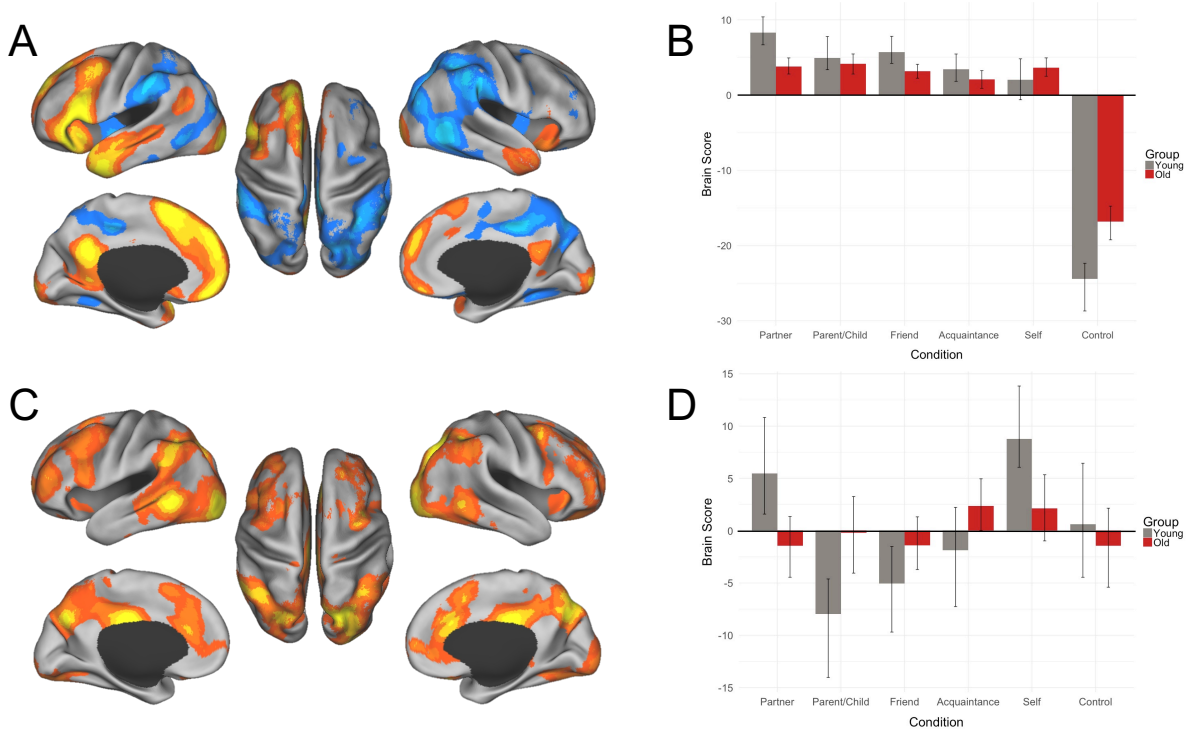

Figure 4.2. Results of the task PLS analysis. A) LV1 activation map, B) LV1 brain scores with 95% confidence intervals, C) LV2 activation map, and D) LV2 brain scores with 95% confidence intervals. PLS analysis for young (grey bars) and old (dark red bars) contrasted activity across partner, parent or child, close friend, familiar acquaintance, self, and control conditions. Warm colors on activation maps (shades of orange and yellow) correspond to positive brain scores, shown by the plotted bars above 0. Cool colors on activation maps (shades of blue) correspond to negative brain scores, shown by the plotted bars below 0. Brain scores represent the cross product of the group result image and the individual subject BOLD response

for each given LV. For activation maps: (*Left*) Lateral and medial views of left hemisphere, (*Center*) Dorsal view, (*Right*) Lateral and medial views of right hemisphere.

The first significant LV accounted for 68.37% of the crossblock covariance (p = 0.002). This LV separated all social other representations and the self from the motor control (number matching) condition for both age groups. This result replicates previous findings that have implicated the default network in mentalizing about others (Krienen, Tu, & Buckner, 2010; Mar, 2011). Significant activations for this first LV were found within dmPFC, vmPFC, PCC, inferior frontal gyrus, superior frontal gyrus, occipital pole, temporal pole, cerebellum, superior temporal sulcus (STS), angular gyrus, fusiform gyrus, middle cingulate gyrus, retrosplenial cortex, hippocampus, and head of caudate (Figure 4.2, Table 4.2.

The second significant LV, accounting for 13.65% of the crossblock covariance (p = 0.002), showed distinct patterns of activation for young and older participants. In young adults, romantic partner and self conditions were differentiated from parent and friend conditions. Activations in anterior insula, dorsal anterior cingulate cortex (dACC), posterior middle cingulate, precuneus, occipital pole, supramarginal gyrus, middle frontal gyrus, posterior middle temporal gyrus, inferior frontal gyrus, superior frontal gyrus, frontal pole, thalamus, orbitofrontal cortex, inferior temporal gyrus, head of caudate, and precentral gyrus were associated with partner and self representations, in the young. In the young participants, the acquaintance and motor control conditions did contribute to the multivariate pattern of activity evidenced by the CIs crossing zero. In contrast, older participants showed a lack of differentiation in patterns of neural response across all conditions and, as such, did not contribute to the multivariate pattern displayed by young adults (Figure 4.2, Table 4.3).

Task-related Functional Connectivity of MPFC

Medial prefrontal cortex is a heterogeneous region central to social cognition. To investigate functional connectivity of MPFC, we ran two seed PLS analyses: first for a dmPFC seed (Figure 4.3) and second for a vmPFC seed (Figure 4.4).

Figure 4.3.

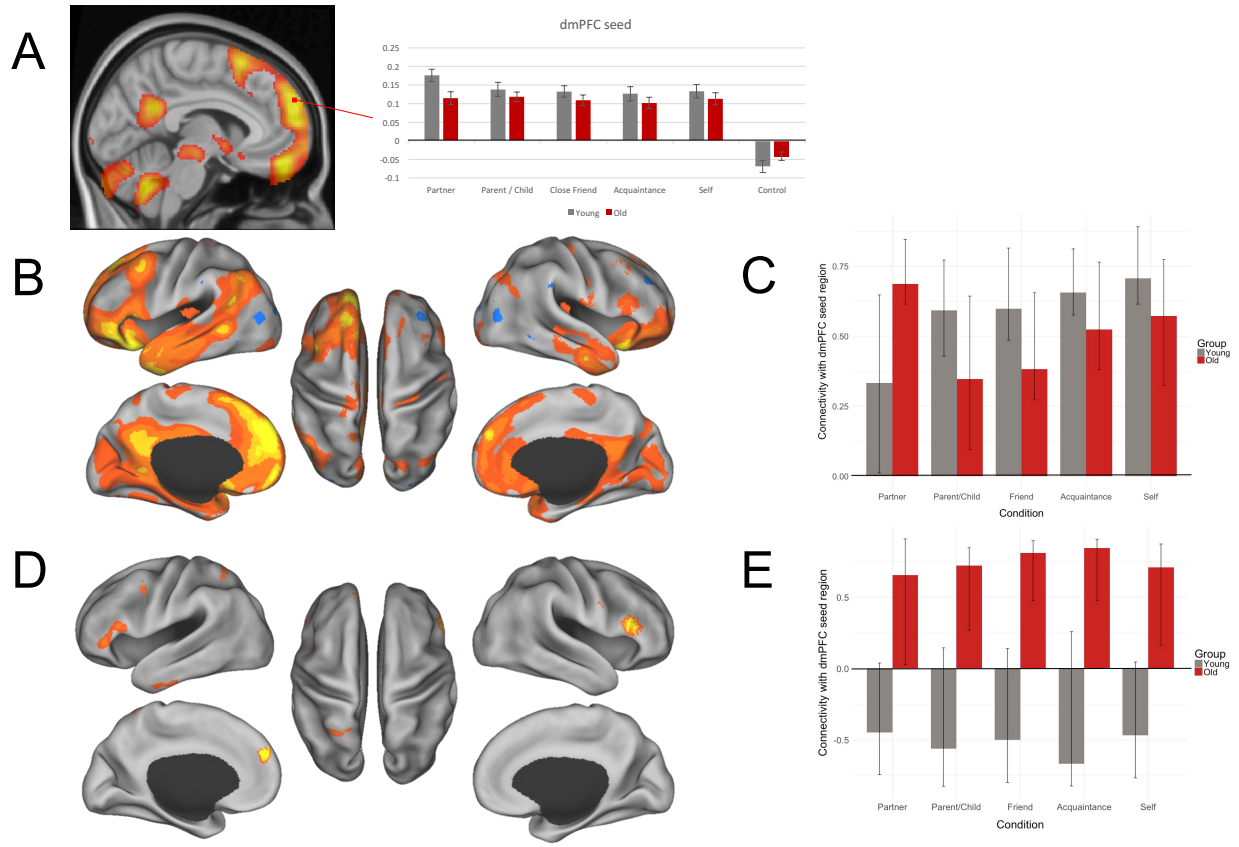

Figure 4.3. Functional connectivity results for dmPFC. A) ROI examining a peak activation seed region within dmPFC. Significance is shown through colors within the bar graphs; grey plotted bars correspond with young adult significant response intensities, and red plotted bars correspond with older adult significant response intensities. B-E) Results of dmPFC seed PLS. B) LV1 connectivity map, C) LV1 condition- and group- wise correlations, with 95% confidence intervals, between the dmPFC seed region and the whole brain pattern of connectivity D) LV2 connectivity map, E) LV2 condition and group correlations, with 95% confidence intervals, between the dmPFC seed region and the whole brain pattern of connectivity. PLS analysis for young (grey bars) and old (dark red bars) contrasted connectivity across partner, parent or child, close friend, familiar acquaintance, and self conditions. Correlations represent the relationship between brain scores for each condition and activity within the dmPFC seed for each condition. Brain scores represent the cross product of the group result image and the individual subject BOLD response for each given LV. For connectivity maps B) and D): Warm colors on connectivity maps (shades of orange and yellow) correspond to positive brain scores, shown by

the plotted bars above 0. Cool colors on connectivity maps (shades of blue) correspond to negative brain scores, shown by the plotted bars below 0. (*Left*) Lateral and medial views of left hemisphere. (*Center*) Dorsal view. (*Right*) Lateral and medial views of right hemisphere.

dmPFC connectivity. The seed PLS analysis for dmPFC revealed two significant LVs: a main effect common to both groups and an age interaction. The first significant LV accounted for 70.21% of the crossblock covariance ($p < 0.000$). This LV demonstrated a shared pattern of connectivity across both young and older adults, within the DN; the dmPFC seed showed robust coactivation with PCC, vmPFC, and STS. Other significant regions functionally connected with dmPFC for this LV were observed in middle temporal gyrus, precentral gyrus, posterior superior frontal sulcus, collateral sulcus, lateral occipital cortex, occipital pole, cerebellum, inferior temporal sulcus, ACC, insula, inferior precentral sulcus, postcentral gyrus, and middle frontal gyrus. (See Figure 4.3).

The second significant LV, accounting for 10.05% of the crossblock covariance ($p < 0.01$), showed a pattern of connectivity that differentiated older adults from young adults. Older adults demonstrated greater connectivity between the dmPFC seed and bilateral lPFC. Other significant regions functionally connected with dmPFC for this LV were inferior frontal gyrus, medial premotor cortex, lateral occipital cortex, vmPFC, middle temporal gyrus, parahippocampus, precentral gyrus, frontal pole, occipital pole, and cerebellum (See Figure 4.3). Connectivity with the dmPFC seed in young adults did not contribute to the multivariate pattern of activity for this LV.

Figure 4.4.

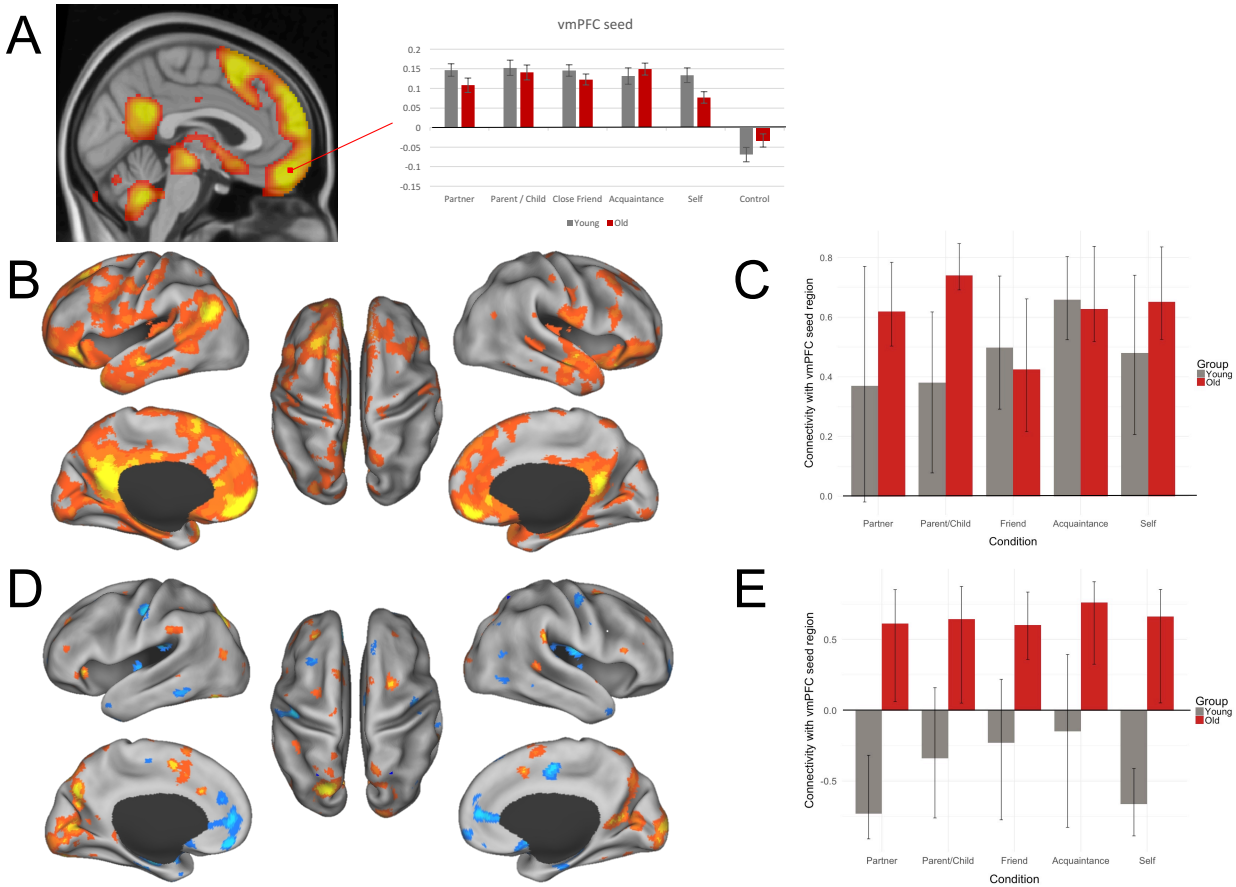

Figure 4.4. Functional connectivity results for vmPFC. A) ROI examining a peak activation seed region within vmPFC. Significance is shown through colors within the bar graphs; grey plotted bars correspond with young adult significant response intensities, and red plotted bars correspond with older adult significant response intensities. B-E) Results of vmPFC seed PLS. B) LV1 connectivity map, C) LV1 condition- and group- wise correlations, with 95% confidence intervals, between the vmPFC seed region and the whole brain pattern of connectivity D) LV2 connectivity map, E) LV2 condition and group correlations, with 95% confidence intervals, between the vmPFC seed region and the whole brain pattern of connectivity. PLS analysis for young (grey bars) and old (dark red bars) contrasted connectivity across partner, parent or child, close friend, familiar acquaintance, and self conditions. Correlations represent the relationship between brain scores for each condition and activity within the vmPFC seed for each condition. Brain scores represent the cross product of the group result image and the individual subject BOLD response for each given LV. For connectivity maps B) and D): Warm colors on connectivity maps (shades of orange and yellow) correspond to positive brain scores, shown by the plotted bars above 0. Cool colors on connectivity maps (shades of blue) correspond to negative brain scores, shown by the plotted bars below 0. (*Left*) Lateral and medial views of left hemisphere. (*Center*) Dorsal view. (*Right*) Lateral and medial views of right hemisphere.

vmPFC Connectivity. The seed PLS analysis for vmPFC also revealed two significant LVs: a main effect common to both groups, and an age interaction. The first significant LV accounted for 73.03% of the crossblock covariance ($p = 0.002$). This LV demonstrated a shared pattern of connectivity across both young and older adults. Activity in the vmPFC seed was positively correlated with activity in PCC/precuneus, ACC, and hippocampus. Other regions that were functionally connected with vmPFC along this LV were observed in posterior middle temporal gyrus, lateral occipital cortex, middle frontal gyrus, thalamus, temporal pole, cerebellum, superior frontal gyrus, temporal pole, frontal pole, posterior supramarginal gyrus, occipital pole, temporal and occipital fusiform cortices, frontal orbital cortex, and brain stem (See Figure 4.4). Connectivity with the vmPFC seed for young adults thinking about their romantic partner did not contribute to the multivariate pattern of activity for this LV.

The second significant LV, accounting for 7.56% of the crossblock covariance ($p < 0.034$), again showed a pattern of connectivity that differentiated older adults from young adults. Older adults demonstrated greater connectivity of the vmPFC seed to regions such as precuneus and dorsal ACC. Other regions that showed significant functional connectivity with vmPFC for older adults only included occipital fusiform gyrus, supramarginal gyrus, occipital pole, frontal orbital cortex, cerebellum, superior frontal gyrus, frontal pole, intracalcarine cortex, and lateral occipital cortex. Young adults, when thinking about their romantic partner or themselves, demonstrated greater connectivity between vmPFC and a different set of regions, such as dmPFC, hippocampus, ACC, insula, and caudate. Other regions that demonstrated greater functional connectivity with vmPFC for these conditions in young adults were subcallosal cortex, postcentral gyrus, parietal and central operculum cortices, SMA, temporal pole, amygdala, frontal pole, inferior temporal gyrus, brain stem, parahippocampus, middle temporal gyrus,

superior frontal gyrus, and precentral gyrus. (See Figure 4.4). Connectivity with the vmPFC seed in young adults thinking about their parent, close friend, or acquaintance did not contribute to the multivariate pattern of activity for this LV.

Discussion

We investigated patterns of brain activity and connectivity associated with mentalizing about known others in younger and older adults, and across levels of social closeness. Consistent with our predictions, the modulation of default network connectivity across levels of social closeness differed for younger and older adults. Whole-brain results showed that for young, default network connections to salience network brain regions differentiated representations of close (self, partner) from more distal social others (see Laurita et al., 2017 for an extended discussion). Patterns of brain response did not differ by level of social closeness for older adults in this analysis. Functional connectivity analyses revealed that for older, but not younger adults, two core default network nodes implicated in the representation of known others (Amodio & Frith, 2006; Heatherton et al., 2006; Mitchell et al., 2006) were persistently coupled with prefrontal brain regions across levels of social closeness. These findings demonstrate that accessing distinct neural representations of known others depends on flexible interactions between the default network and other large scale brain systems.

Dedifferentiated representations of social others in older adulthood

For both age-groups increased activation of dmPFC, vmPFC, and PCC, was observed across all social-other conditions, but not the motor control condition. These brain regions form part of the "social brain" (Mitchell, 2008) and are core nodes of the default network (Buckner et al., 2008; Andrews-Hanna et al., 2014). In the whole-brain analysis, default network interactions with the salience network in the young group differentiated mentalizing about close versus more

distal others. In contrast, default network interactivity was not modulated by social closeness in the older group, suggesting that neural representations of social others may become increasingly dedifferentiated in later life.

These results suggest that default network engagement alone may be necessary but insufficient to instantiate the full spectrum of relationships in our social milieu. As demonstrated in our young group, default network interactions with other brain systems, such as the salience network, may be required to form more detailed or differentiated representations of social others. While the current study assessed only a single dimension of 'closeness' based on levels of attachment, there are myriad determinants of how social closeness may be represented in the brain (see Thornton and Mitchell, 2017 for a recent discussion). These may include perceptual (e.g. personal similarity); affective (e.g. attachment or affection); or more cognitively-based discriminations (e.g. demographic or socio-economic factors). While beyond the focus of the current report, we suggest that dynamic default network interactions with other large scale brain systems implicated in these domains may be necessary to instantiate and update neural representations of these complex, multi-dimensional features of social others.

In this context, here we speculate that the absence of neural differentiation for socially close others in the older adult group may reflect reduced flexibility and thus poor interactivity of the default network with salience network brain regions which are implicated in close personal attachment relationships. There is growing evidence of reduced default network dynamics in older adulthood (Spreng and Schacter, 2012; Turner and Spreng, 2015; Rieck et al., 2017). Further, we have recently shown that greater intrinsic default network coupling with executive brain regions is associated with less detailed or more semanticized autobiographical recollection (Spreng et al., in review). Here we suggest that representations of social others may also become

less differentiated and more schema-based as default network interactivity is reduced or becomes less flexible in later life.

Default network interactivity and social other representations in older adulthood

We implemented targeted task-related functional connectivity analyses to investigate age-related differences in connectivity of two core default network nodes in the dmPFC and vmPFC. These regions have been consistently implicated in mentalizing about the identity, characteristics or thoughts of known others (Gobbini et al., 2004; Krienen et al., 2010; Moran et al., 2012; Thornton and Mitchell, 2017; Hassabis et al., 2014). They also represented peak activations in our trait judgment versus control task analysis (Figure 4.2). Consistent with our earlier findings, and previous research implicating the default network in mentalizing and social cognition (Krienen et al., 2010; Mitchell et al., 2008), both dmPFC and vmPFC nodes were functionally connected with other default network brain regions for all levels of social closeness in both groups.

Critically however, each analysis revealed a second significant pattern of functional connectivity that was reliable only in the older adult group. For both seed regions, older adults demonstrated functional connectivity with prefrontal regions bilaterally (Figures 4.3D and 4.4D). This pattern of age-related recruitment of prefrontal brain regions, and engagement of the default network, is commonly observed in neurocognitive aging studies. We have demonstrated that these processes are coupled and poorly modulated by task context (Turner and Spreng, 2015) in older adults. This pattern of default-executive coupling has now been replicated during both task and rest, and is associated with reduced fluid reasoning abilities (Rieck et al., 2017) and increased semantic cognition (Spreng et al., submitted) in older adulthood.

With respect to the current findings we suggest that engagement of frontal cortices, necessary for cognitive control, coupled with default network brain regions, critical for social cognition, may support mentalizing about social others in older adulthood. However, as can be seen clearly in Figures 3E and 4E, there is no differentiated pattern of functional connectivity between these default network seed regions and prefrontal cortices across the continuum of social closeness. As we have argued above, this may reflect reduced default network dynamics in older adulthood. In young adults, neural representations of social closeness were associated with differentiated patterns of default network coupling. However, in older adults core nodes of the default network remained functionally coupled with frontal brain region across all levels of social closeness, resulting in dedifferentiated neural representations of social others.

Here we have shown that the neural representation of close others is altered in older versus younger adults. With age, representations across the spectrum of social closeness, from the self and romantic partners, to more socially-distant acquaintances, become dedifferentiated. We also observed that older adults engage both default network and frontal brain regions while mentalizing about known others. We speculated that for older adults, greater control processes may be required to mentalize, or access known-other representations. However this compensation likely comes at a cost. Greater default – executive coupling and reduced flexible interactivity with other large-scale brain systems may result in degraded or poorly differentiated representations of personally known others.

Study limitations

In the current study we have defined social closeness based on a model of attachment and perceived inclusion of other in the self. However, as noted above, there are multiple dimensions along which closeness may be stratified, including demographic factors, perceived similarity,

fondness, and dyadic relatedness. As suggested recently by Thornton and Mitchell (2017) representations of close others based on these different schema may have distinct neural signatures and thus represents an interesting and important line of future research. Further, we elected to investigate neural network dynamics across the continuum of known others, potentially limiting the generalizability of the work to investigations of known versus unknown others. We explicitly drew this experimental distinction as we were specifically interested in investigating a range of closeness for known others. Adding an anonymous other would have represented a categorical distinction that, while theoretically important, was not a primary focus of the work. Finally, we recognize the limitations of an extreme groups design and the absence of a true lifespan sample. However, we continue to pursue this program with the ultimate goal of collecting subject from each decade of life to investigate the network neuroscience of social cognition and mentalizing across the full adult lifespan.

Conclusions and implications

Taken together, our findings highlight the importance of investigating neural network dynamics in the study of neurocognitive aging. In fact our findings suggest that well-established network neuroscience models of brain aging may be readily extended to studies of social aging neuroscience. On a final cautionary note, our results raise an important point with respect to social cognition in later life. These data suggest that while older adults may be able to recruit cognitive control resources to successfully mentalize about others, reduced network dynamics may result in degraded social-other representations. These functional brain changes, whether occurring in the context of normal aging or brain disease, may lead to inaccurate predictions, and thus inadequate cautions, with respect to the actions or intentions of others in their social milieu.

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Table 4.1. Descriptive Statistics for Self-Report Measures

Measure	Romantic Partner	Parent/Child	Close Friend	Acquaintance
WHOTO *(M, SD)* Out of 40	Young: 32.83, 6.80	Young: 22.31, 8.46	Young: 6.97, 7.56	-
	Older: 36.70, 6.59	Older: 17.04, 9.65	Older: 4.70, 5.59	-
IOS *(M, SD)* Out of 7	Young: 4.83, 1.23	Young: 2.93, 1.39	Young: 2.97, 1.55	Young: 1.55, 0.69
	Older: 5.22, 1.45	Older: 3.52, 1.50	Older: 2.89, 1.53	Older: 2.30, 1.38

Table 4.2. Peak Activation Coordinates, LV1

Region	Coordinates			
	x	*y*	*z*	BSR
Social > Control				
Dorsomedial prefrontal cortex	-8	54	32	-16.44
Inferior frontal gyrus	-56	24	12	-15.44
Superior frontal gyrus	-4	14	54	-14.84
Posterior cingulate cortex	-6	-54	30	-12.55
Occipital pole	-22	-98	0	-12.02
Temporal pole	-44	6	-38	-11.59
Cerebellar Crus I	24	-82	-32	-11.46
Ventromedial prefrontal cortex	-2	50	-18	-11.23
Superior temporal sulcus	-48	-36	-2	-7.31
Temporal pole	48	10	-34	-6.97
Angular gyrus	-46	-62	24	-6.70
Fusiform gyrus	-38	-44	-22	-5.03
Middle cingulate gyrus	-2	-14	36	-4.71
Retrosplenial cortex	18	-48	4	-4.49
Hippocampus	-24	-28	-6	-4.12
Cerebellar Crus I / Crus II	-32	-82	-36	-3.83
Inferior frontal gyrus	36	22	18	-3.47
Head of caudate	18	10	14	-3.42
Control > Social				
Middle cingulate gyrus	10	-36	44	12.57
Superior parietal lobule	34	-48	44	10.50
MT+	52	-58	-8	10.45
Superior parietal lobule	-38	-42	42	9.43
Cerebellar VIIB	-18	-74	-46	8.91
MT+	-52	-60	-6	8.86
Insula	-40	-10	-4	8.45
Ventral precentral sulcus	50	2	8	7.89
Dorsolateral prefrontal cortex	36	40	24	7.35
Frontal eye field	24	8	56	6.61
Frontal pole	44	40	4	6.56
Dorsolateral prefrontal cortex	-30	30	34	6.42
Inferior temporal gyrus	-52	-32	-22	6.40
Cerebellar VIIIB	18	-58	-52	6.24
Superior frontal gyrus	-22	6	56	4.84
Frontal pole	22	68	-2	3.74

Table 4.3. Peak Activation Coordinates, LV2

Region	Coordinates			BSR
	x	*y*	*z*	
For Young Only: Partner and Self > Parent and Friend				
Precuneus	-8	-68	38	6.71
Occipital pole	-22	-96	-4	6.68
Supramarginal gyrus	46	-40	32	6.56
Posterior middle cingulate	8	-24	32	6.54
Middle frontal gyrus	40	8	54	5.79
Posterior middle temporal gyrus	52	-50	-4	5.27
Supramarginal gyrus	-42	-48	34	5.21
Inferior frontal gyrus	-60	18	12	4.98
Dorsal anterior cingulate cortex	10	30	26	4.95
Superior frontal gyrus	16	12	52	4.77
Frontal pole	-40	48	10	4.48
Thalamus	24	-28	0	4.45
Orbitofrontal cortex	-14	30	-24	3.89
Inferior temporal gyrus	-58	-16	-40	3.85
Head of caudate	-12	22	-6	3.84
Anterior insula	30	18	-8	3.54
Precentral gyrus	62	16	14	3.36
Anterior insula	-24	24	-6	3.27

CHAPTER 5

Neural signatures of chronic accessibility in parent – adult child attachment bonds

Our most critical bonds are often formed with our parents and children. These stable relationships, often conceptualized as attachment bonds, are characterized by feelings of security with affect-regulatory benefits (Hazan et al., 2004; Sroufe & Waters, 1977; Pietromonaco et al., 2006). Ethological attachment is theorized to necessitate proximity maintenance to caregivers, promoting chances of infant survival (Bowlby, 1982). Early observational studies of toddlers demonstrated parental attachment figures' role in soothing separation-related distress upon reunion (Ainsworth et al., 1978), and recent work highlights parents' neurobiological response to their children's distress (Noriuchi et al., 2007; Swain et al., 2014). The parent-child attachment bond is uniquely reciprocal, consistently demonstrating biobehavioral synchrony, or the sensitization to and coordination of physiological and behavioral responses (Feldman, 2012). Moreover, this relationship is capable of persisting as both child and parent age and adapt to shifts in behavioral dynamics related to role-reversal (Ainsworth, 1989; Carpenter, 2001).

Inherent to parent-child attachment bonds are the mental representations, or internal working models, of these figures that come about due to reward conditioning. Lack of perceived proximity to an attachment figure engages the mental representation of that figure, providing comfort and security. Importantly, attachment figure mental representations exhibit chronic accessibility (Andersen, et al. 1990; Baldwin et al., 1993); they are easy to bring to mind and readily available for utilization in the face of stressors, requiring fewer cognitive resources overall. Because of the powerful reciprocal roles of parental and adult child attachment figures, it is likely that their chronically accessible mental representations have unique neural signatures. Limited existing work examines patterns of neural activity underlying mentalizing for, or

imagining the thoughts and feelings of, these attachment figures. Mothers viewing photos of their own child versus an unfamiliar child, recruit insula, amygdala, anterior paracingulate cortex, and superior temporal sulcus; mothers viewing an unfamiliar child versus their own show increased activity in regions related to attention, including intraparietal sulcus and precuneus, and face perception, such as fusiform gyrus (Leibenluft et al., 2004). Young adults making trait judgments for parents engage default network regions of dorsomedial and ventromedial prefrontal cortex, and posterior cingulate cortex (Laurita et al., 2017). Bringing to mind mothers versus close friends recruits medial prefrontal cortex and anterior cingulate cortex, demonstrating that parent-child attachment may modulate engagement of these regions (Wang et al., 2012). Research investigating brain activity for chronically accessible parents and children could provide crucial support for the cognitive benefits of responsive parenting practices (Feldman, 2012), especially in clinical populations challenged by social attunement, such as children with autism (Baker et al., 2015).

Here we use fMRI to examine the neural representation of young adults' parents and older adults' children. We sought to determine how mental representations of parents and children are associated with differential patterns of brain activity, modulated by attachment. Based on the chronic accessibility of attachment figure mental representations, we predicted that bringing to mind attached parents or children would require fewer neural resources, as measured by decreased activation across various neural systems as a function of attachment.

Materials and Methods

Participants

Participants were 29 healthy, right-handed young adults (16 females, 13 males;

M age = 24 years, *SD* = 3.5 years) and 27 healthy older adults (12 females, 15 males; *M* age = 67 years, *SD* = 6 years), with normal or corrected-to-normal visual acuity. Participants had no history of psychiatric, neurological, or other medical illness that could compromise cognitive functions. Although data were collected from 59 subjects, 3 subjects were excluded from subsequent analyses: 2 young adults for noncompliance and 1 older adult due to brain abnormalities. In accordance with the Institutional Review Board of Cornell University, participants gave written informed consent prior to scanning.

Assessment of Attachment to Parent/Child

We recruited from a pool of eligible individuals, asking that young adult participants have a living parent to whom they felt close and older adult participants have an adult child to whom they felt close. Participants completed a pre-scan survey about their various personal relationships, including their relationships with their specific parent or child. Participants first provided one name per relationship condition in response to prompts (see Laurita et al., 2017 for information regarding pre-scan survey). This survey included a self-report measure of attachment (WHOTO; Fraley & Davis, 1997; Hazan et al., 1991) and relationship length. The WHOTO is an attachment functions measure that determines the people with whom subjects display attachment relationships. Items are based on four attachment features: proximity seeking, separation distress, safe haven, and secure base. Subjects list up to four most important figures in their lives for each of the ten items. The WHOTO can be used in various ways to measure individuals' attachment to others. In the present study, we utilized it as a continuous measure of attachment with parent or child (in contrast to attachment with romantic partner and close friend) by scoring each item based on the individual's ranking (highest scores = listed first) and totaling these scores; therefore higher WHOTO total scores were indicative of greater levels of attachment.

Task and fMRI Design

During fMRI scanning, we used a trait-judgment task in which participants were asked to think about several people in their lives mentioned by name in the pre-scan survey. Each trial contained a trait adjective and a person's name; participants rated the person on each trait adjective, on a scale of 1 (unlike this person) to 3 (very much like this person). Blocks were composed of 5 trials in which participants were instructed to hold the person in mind continuously while making each trait judgment about that person. Trait judgments were also made for a romantic partner, friend, acquaintance, famous person, and the self, but are not considered in the current report. See Figure 5.1 for behavioral paradigm. Additional details regarding the task and fMRI can be found in the Supplemental Material.

Figure 5.1.

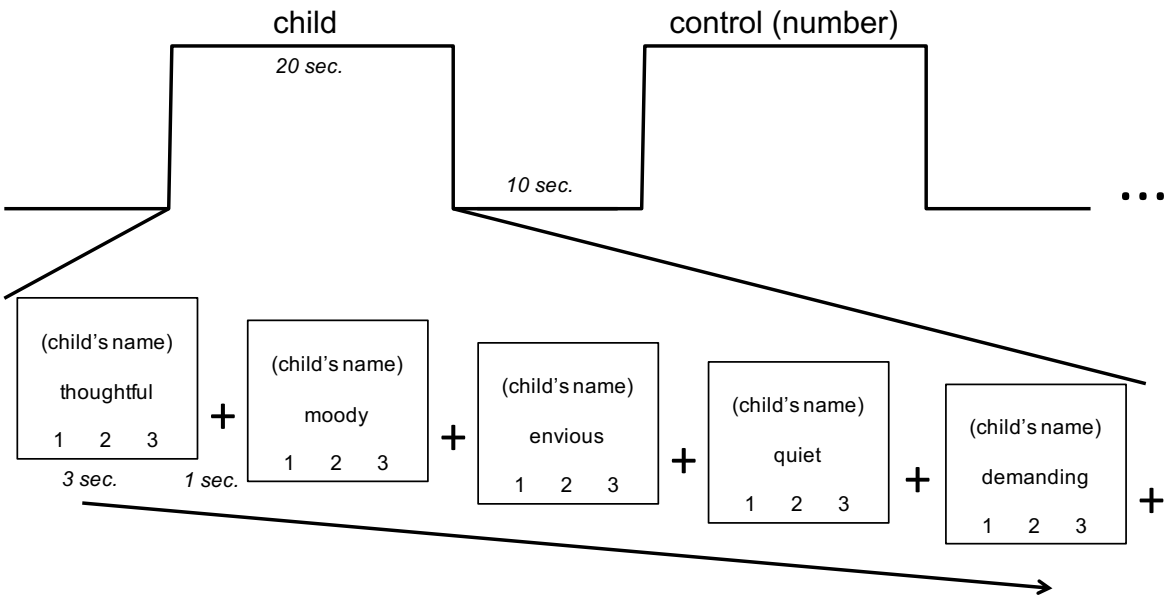

Figure 5.1. Behavioral paradigm, involving trait-judgment task. "Child" condition was shown to older adults.

Magnetic Resonance Image Acquisition

Brain imaging data were acquired using a 3T GE Discovery MR750 MRI scanner with a 32-channel head coil. This MRI scanner was located within the Cornell Magnetic Resonance Imaging Facility in Ithaca, New York. Anatomical scans were acquired using a T1-weighted volumetric MRI magnetization prepared rapid gradient echo (TR = 7.7 ms; TE = 3.4 ms; 7° flip angle; 1.0 mm voxels with no gap, 176 slices). Five 7 m 40 s experimental runs of blood–oxygen level dependent (BOLD) functional scans were acquired with a T2*- weighted multi-echo imaging pulse sequence (TR = 2000 ms; TEs = 12.7, 27.5, and 43 ms; 77° flip angle; 33 axial slices; matrix size = 64 x 64; field of view (FOV) = 240 mm; 33 axial slices; 3.8 mm thick slices).

Preprocessing of Magnetic Resonance Imaging Data

BOLD fMRI data were preprocessed to correct for motion, physiological noise and scanner artifacts using Multi-Echo Independent Components Analysis (ME-ICA) with meica.py (Kundu et al., 2012). ME-ICA is a method for de-noising fMRI data based on information about the T2* decay of the BOLD signal, acquired through multi-echo fMRI. Using ME-ICA, multi-echo fMRI datasets can be decomposed into independent components before these components are categorized as BOLD or noise/non-BOLD. ME-ICA robustly de-noises fMRI data by removing all non-BOLD components (Kundu et al., 2012; Lombardo et al., 2016). The BOLD fMRI images were normalized to a custom young-old population template derived from 50 young (25 female; *M* = 22.02y, *SD* = 3.13y) and 50 older (25 female; *M* = 67.14y, *SD* = 6.7y) adults. Included template subjects were selected from an in-house brain bank for low trait motion, as recent work has indicated that trait motion can bias structural scans (mean FD = 0.09; Savalia et al., 2017). Anatomical images for included subjects were affine registered to MNI space using *@toMNI_Awarp* before being non-linearly, iteratively aligned

using *@toMNI_Qwarpar* in AFNI. Data were resampled to 2x2x2-voxel volumetric time-series and smoothed with an 8-mm full width half maximum (FWHM) Gaussian kernel.

fMRI Analysis

Partial Least Squares

Analyses were performed using partial least squares (PLS; Krishnan et al., 2011; McIntosh et al., 2004), a multivariate functional neuroimaging analysis technique used to identify whole-brain patterns of activity that are correlated with task. PLS identifies a set of orthogonal latent variables that optimally relate BOLD signal and the experimental design or a measure of behavior. PLS results can be interpreted as identifying covarying sets of brain regions in which activity is reliably associated with a specific condition, or where brain activity during a condition of interest covaries with offline behavior, such as WHOTO scores.

For each analysis, the significance of each latent variable was determined by permutation testing, using 500 permutations with random reordering of the task conditions for each participant. PLS is recalculated for each permutation sample, and the frequency in which the permuted singular value exceeds the observed singular values is determined and expressed as a probability. The reliability of the saliences for the brain voxels across participants, characterizing each pattern identified by a latent variable, was determined by bootstrap resampling with replacement, using 100 iterations, to estimate the standard errors for each voxel. We set a minimum bootstrap ratio (conceptually similar to a Z-score) at 2.58 equivalent to $p < 0.01$. In the current sample, fifty-six total subjects gives us 80% power to detect effect small effect sizes, $r > 0.25$. Because analyses analysis is performed across voxels in a single analytic step, no correction for multiple comparisons is required. Additional details regarding PLS can be found in the Supplemental Material available online.

Results

Behavioral Results; Assessment of Attachment to Parent/Child

First, we confirmed that parents and children are significant attachment figures. We note that levels of attachment varied across our sample, permitting an assessment of individual differences. See Supplemental Material for results of ANOVA tests across WHOTO total scores. To compare across parent and child conditions, we also examined length of relationship for young adults with their named parent and older adults with their named child. Although our sample of parents and children were not related, younger participants' ages were not significantly different from that of the older adults' children ($t_{(26)} = -1.91$, $p = 0.07$, $d = 0.55$). Although developmentally very different, this suggests that the parent-child relationship was of similar length between our groups. Descriptive statistics for WHOTO and relationship length are in Table 5.1.

Neuroimaging Results

Brain activation during mentalizing about one's parent or child, relative to the control condition, engaged the default network ($p = .002$; see Supplemental Figure 5.S1), consistent with prior reports of mentalizing (e.g., Mar, 2014). Central to the aims of the current study, brain activation when mentalizing about one's parent or child significantly varied as a function of attachment ($p = .016$, 78.08% crossblock covariance explained). A significant negative association was observed between WHOTO scores and activity in a number of brain regions. Results showed that the more attached one feels to their parent or child, the lower brain activity was observed in anterior cingulate cortex (ACC), left amygdala hippocampus, anterior and posterior insula, posterior cingulate cortex (PCC), and the putative occipital face area (OFA), as well as other regions (Figure 5.2; see Table 5.2 for full results).

Figure 5.2.

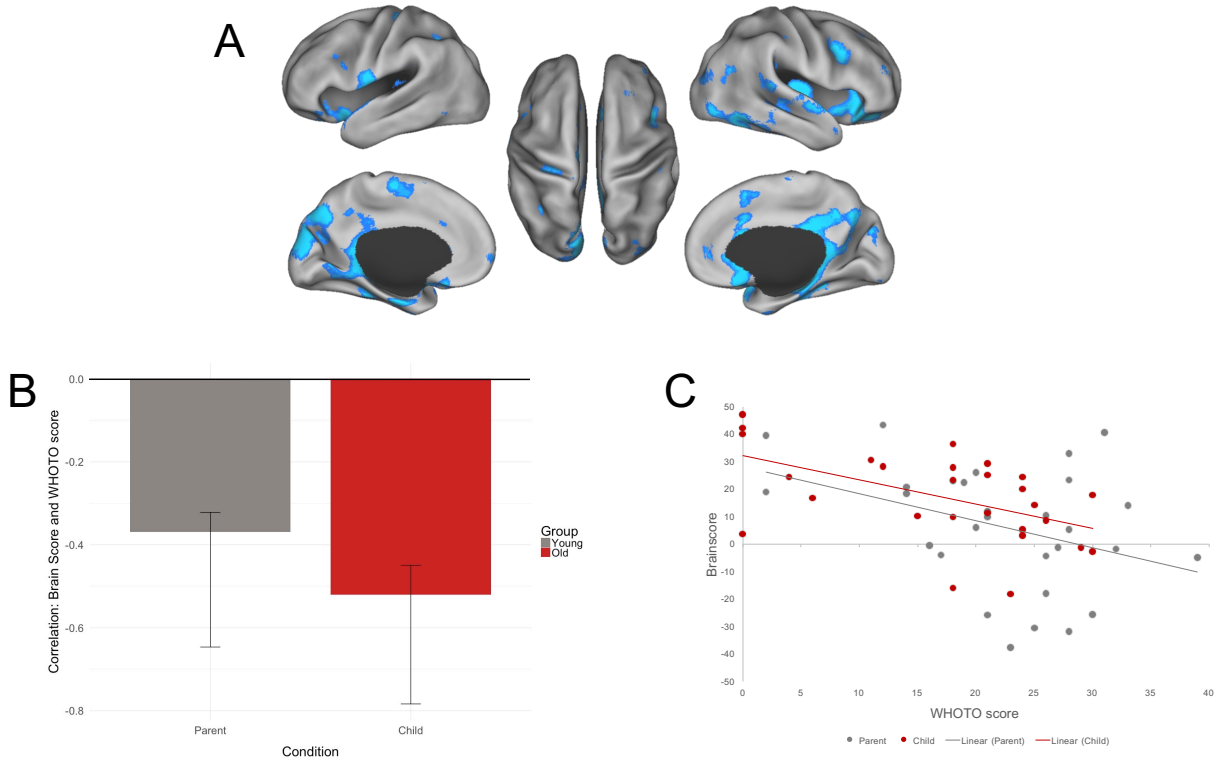

Figure 5.2. Relationship between parent/child attachment and brain activity while mentalizing. A) Significant reductions in brain activity as a function of attachment when making trait judgments about parent or child. B) Bootstrapped correlation values between a composite measure of brain activity and the WHOTO score for each group, revealing similar magnitude of covarying activity in both younger and older adults. C) Scatterplot of the association between a composite brain activity score (depicted in A) and attachment (measured by the WHOTO).

Discussion

The present study identified brain regions whose activity varies as a function of attachment. During mentalizing about attachment figures, one's parents or children, brain activity was systematically reduced as a function of perceived closeness. Put another way, when we think about our parents or children, reduced brain activity is observed when we are more bonded to these figures. Importantly, brain regions identified as showing lower activation with higher levels of attachment serve important roles in social navigation (e.g., Tavares et al., 2015). This inverse relationship between brain activity and attachment scores provides the first empirical support for a neural mechanism underlying the chronic accessibility of attachment figure mental representations. Conditioning to the presence of an attachment figure allows us to readily access our representations of that person without taxing cognitive and neural resources.

Mental representations of attached parents and children comprise highly salient experiences and, as such, are differentiable from other social mental representations. Decreased activation was observed in regions implicated in past findings on attachment figure representations. ACC and insula activity is associated with distress and pain alleviation by close others (Coan et al., 2006). These regions are involved in the salience network (Seeley et al., 2016), a collection of brain regions that coordinates responses to meaningful environmental stimuli (Uddin, 2015). PCC is a known default network hub, recruited in social cognitive processes, such as mentalizing, for close others (e.g., Krienen et al., 2010; Laurita et al., 2017). Results of the present study add nuance to the association between default network activity and social closeness; one interpretation of the convergence of these findings would be that PCC remains online while individuals cognitively represent non-attached social others. Decreased activation of left amygdala with greater attachment is likely related to the region's processing of

fear versus safety signals (Phelps et al., 2001). The hippocampal memory system plays a role in social cognition, specifically in integrating information on relative social affiliation and power (Tavares et al., 2015; for review, see Laurita & Spreng, 2017). Our results provide evidence that hippocampus-supported social memory is necessitated only by less chronically accessible close others. OFA is putatively implicated in face perception and, particularly, in recognition of unfamiliar faces and objects (Gauthier et al., 2000); less recruitment of OFA for attached parents and children supports chronic accessibility, as these figures are easily recognizable and highly familiar.

These findings enhance our understanding of the neural representation of some of the most important people in our lives—parents and children—and illuminate how attachment modulates these representations. The profound impact of attachment figure representations on individuals' affective and physiological regulation (Pietromonaco et al., 2006) and expectations for social-other responsiveness in future interactions (Anderson & Cole, 1990) is already well-documented. The present results provide novel evidence that one critical evolutionary advantage of attachment bonds is the conservation of valuable neural and cognitive resources in conferral of regulatory benefits. Attachment figures need not be physically present to promote our well-being and, by merely bringing them to mind we can alleviate the cognitive load of social processing. Future work should explore this neural mechanism for chronic accessibility as it relates to our ability to navigate the complex social world around us.

Author Contributions

All authors, A. C. Laurita, C. Hazan, and R. N. Spreng, developed the study concept and contributed to the study design. A. C. Laurita performed data collection and analysis under the supervision of R. N. Spreng. A. C. Laurita and R. N. Spreng contributed to interpretation of the data. A. C. Laurita and R. N. Spreng wrote the paper. All authors approved the final version of the manuscript for submission.

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Table 5.1. Descriptive Statistics for Self-Report Measures

Measure	Parent (Young Adults)	Child (Older Adults)
WHOTO *(M, SD)* Out of 40	22.31, 8.46	17.04, 9.65
Length of Relationship *(M, SD)* In years	22.90, 4.81	29.27, 2.44

Table 5.2. Peak Activation Coordinates

Region	Coordinates			BSR
	x	*y*	*z*	
Decreased activity as a function of attachment to Parent or Child				
Dorsal anterior cingulate cortex	14	24	26	7.33
Brain stem	6	-34	-12	6.71
Orbitofrontal cortex	2	24	-32	6.44
Amygdala	-22	4	-18	6.20
Supramarginal gyrus	44	-26	32	6.00
Posterior insula	42	-14	10	5.77
Inferior temporal gyrus/ Occipital face area	56	-58	-18	5.66
Cuneus	4	-86	34	5.35
Superior parietal lobule	-28	-52	46	5.21
Posterior cingulate cortex	4	-42	40	5.04
Parahippocampus	-18	-12	-30	4.86
Lateral occipital cortex	44	-64	28	4.85
Precentral sulcus	42	-4	38	4.81
Hippocampus	24	-26	-16	4.67
Superior temporal gyrus	64	-2	-10	4.66
Occipital fusiform gyrus	28	-82	-18	4.60
Thalamus	-18	-22	-2	4.49
Fusiform gyrus	-32	-36	-20	4.45
Insula	-36	6	18	4.36
Poster superior temporal sulcus	66	-42	10	4.29
Anterior fusiform gyrus	-30	-2	-48	4.29
Cerebellar vermis	-8	-66	-40	4.22
Anterior insula	26	22	-2	4.19
Occipital face area	-50	-68	-14	4.13
Dorsal anterior cingulate cortex	-14	22	34	4.04
Precentral gyrus	-54	0	2	3.94
Frontal pole	-10	68	-4	3.94
Orbitofrontal cortex	-16	30	-18	3.81
Precentral gyrus	0	-18	66	3.81
Superior frontal gyrus	-18	34	36	3.79
Frontal pole	44	54	16	3.78
Hippocampus	-36	-24	-12	3.75
Lateral occipital cortex	36	-78	4	3.72
Middle frontal gyrus	30	36	50	3.70
Lateral occipital cortex	36	-84	24	3.68

Supplementary motor area	8	10	56	3.67
Anterior insula	-42	26	10	3.41

Supplemental Material

Task and fMRI Design

Blocks were interleaved with 10 seconds of fixation. We also included a motor control condition block, in which participants were prompted with "Which number?", shown a number 1, 2, or 3, and instructed to respond by pushing the button corresponding to that number.
The experiment consisted of 350 trials divided across 5 runs, each consisting of 14 blocks, in turn comprising 5 trials per block. Trials were 3-seconds long, and a 1-second crosshair fixation screen appeared between each trial. There were 2 blocks per run for each of the conditions. The order of conditions within each run was randomized. Each task run lasted 7 minutes and 40 seconds. The 5 runs were then counterbalanced for each participant to eliminate any possibility of ordering effects of the fixed condition order and adjective order.

50 trait adjectives were selected for the study in order to ensure that each word was used exactly once for each condition. The trait adjectives were selected from a list of popularly used personality terms. The trait adjectives were presented in a fixed order across blocks, such that each trait adjective was paired exactly once with each condition.

Partial Least Squares

PLS is sensitive to a distributed voxel response, rather than the activity of individual voxels per se, and assesses the covariance between brain voxels (BOLD signal) and the experimental design to identify a limited number of orthogonal components (LVs) that optimally relate the two. This data-driven approach determines orthogonal whole-brain patterns of activity that covary with the experimental design. Within the PLS framework, brain activity is constrained to examine the covariance between brain activity and task design. In this regard, we are able to examine robust patterns of activity only associated with the experimental conditions.

Along these same lines, PLS is capable of analyzing multiple conditions simultaneously to examine covariance of response across conditions. The current study design was optimized for a PLS analysis to assess distributed patterns of activity across conditions.

Activity for each voxel was averaged across blocks for both parent and child conditions and normalized relative to activity at fixation preceding the trait judgment. The data matrix was expressed as a voxel-by-voxel deviation from the grand mean across the entire experiment, which was decomposed using singular value decomposition to derive the LVs representing task contrasts. Each brain voxel is given a singular value weight, known as a salience (akin to a component loading in principle component analysis), which is proportional to the covariance of voxel activity with the task contrast represented by each LV. Multiplying the salience by the BOLD signal value in that voxel and summing the product across all voxels gives a composite brain activity score for each participant on a given LV.

Behavioral Results

We conducted repeated measures ANOVA tests across WHOTO total scores. In the young adults, there was a significant difference between means of parent, romantic partner, and close friend WHOTO scores ($F(2, 56) = 68.00$, $p < 0.001$). Results of non-parametric analyses mirrored these ANOVA results, as a Friedman test yielded significant differences among repeated measures χ 2 (2, $N = 29$) = 40.55, $p < 0.001$. In the older adults, results also showed a significant difference between means of child, romantic partner, and close friend WHOTO scores ($F(2, 52) = 127.96$, $p < 0.001$). Results of non-parametric analyses mirrored these ANOVA results, as a Friedman test yielded significant differences among repeated measures χ^2 (2, $N = 27$) = 44.24, $p < 0.001$. We conducted both non-parametric tests to account for alternative perspectives that consider WHOTO scores as ordinal data. We ran several post-hoc t-tests to

clarify the nature of attachment-related differences between parents/children in comparison to participants' other close social relationships. Young adult participants reported significantly greater attachment to parents over friends ($t_{(56)} = 7.28$, $p < 0.001$, $d = 1.91$), and older adults also reported significantly greater attachment to children over friends ($t_{(42)} = 5.75$, $p < 0.001$, $d = 1.56$). Results also showed, however, that young adult participants reported significantly greater attachment to romantic partners over parents ($t_{(56)} = 5.22$ $p < 0.001$, $d = 1.37$). Older adult participants also reported significantly greater attachment to romantic partners over children ($t_{(46)} = 8.74$, $p < 0.001$, $d = 2.38$). Taken together, these results demonstrate that participants' parents or children served as attachment figures, whereas close friends were not attachment figures for our participants.

Neuroimaging Results

The supplementary task PLS analysis investigated neural activity for parent or child and motor control conditions. This PLS analysis revealed one significant pattern of activity, or latent variable. This significant LV accounted for 91.53% of the crossblock covariance ($p < 0.000$). Brain scores for parent and child conditions covaried against the control condition. Significant activations for this LV were found within ventromedial and dorsomedial prefrontal cortex, posterior cingulate cortex, superior temporal sulcus, inferior frontal gyrus, occipital pole, cerebellum, caudate, lateral occipital cortex, frontal orbital cortex, brain stem, and temporal occipital fusiform cortex. (Figure 5.S1).

Figure 5.S1.

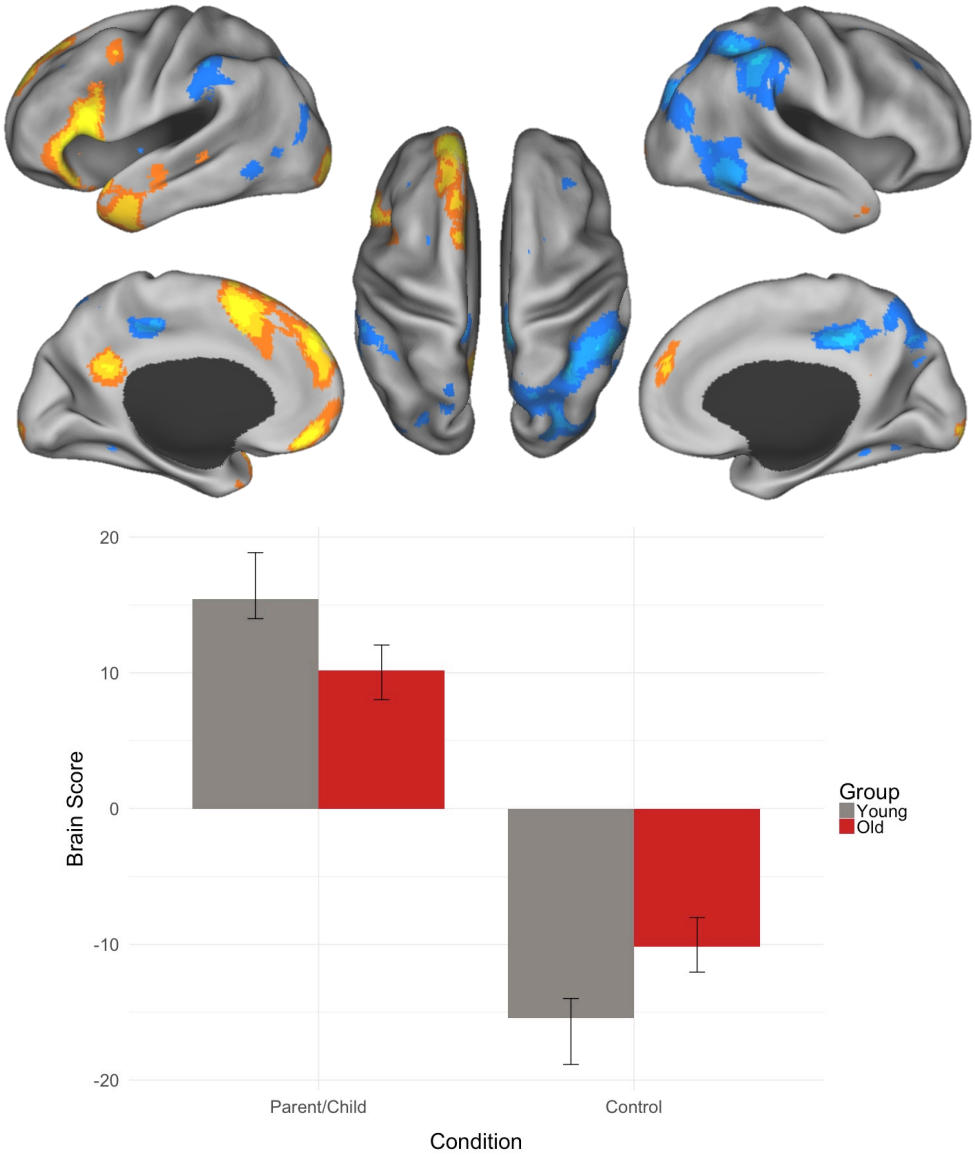

Figure 5.S1. Results of the PLS analysis comparing activity across parent/child and control conditions; LV Activation map (*Top*) and brain scores with 95% confidence intervals (*Bottom*). Cool colors on activation maps (shades of blue) correspond to negative brain scores. For activation map: (*Left*) Lateral and medial views of left hemisphere. (*Center*) Dorsal view. (*Right*) Lateral and medial views of right hemisphere.

CHAPTER 6

Conclusions

The present dissertation investigated the neural representation of close others across adulthood. Chapter 2 demonstrated the applicability of attachment theory in understanding how cognitive representations of close others might be vastly different from other social neural representations. In addition, this review highlighted the variety of neuroimaging findings resulting from and methods involved in past research. Finally, this chapter provided recommendations for the emerging field of close relationship neuroscience. Chapter 3 served as an initial empirical test of the premises laid out in Chapter 2. Making trait judgments for known others along a spectrum of closeness resulted in differential brain activity, and attachment was a distinguishing feature of these differences. Chapter 4 extended this line of research further, into social aging neuroscience, as it investigated mentalizing for known others in both young and older adults. Neural representations of close others became less differentiated in older adulthood, and connectivity patterns showed differential coupling in older adults, as well. Chapter 5 directly investigated the modulatory effect of attachment on brain activity for parents and adult children. Bringing to mind one's attached parent or child required less engagement across a variety of brain regions, which provided preliminary evidence for unique neural signatures of chronic accessibility. Directions for future research specific to each line of work have been discussed in each of the preceding chapters, respectively. The last section of this dissertation raises broader directions for promising research related to findings presented in the previous four chapters.

Methodological Advancements in the Study of Neural Representations of Close Others

The literature discussed in Chapter 2 provided evidence for how the brain represents close social others; however, this review also gave insight into all that we still do not know. First,

it will be crucial to apply an interdisciplinary, multi-method approach for mapping the neural representation of real-world attachment figures. Across Chapters 3, 4, and 5, a consistent fMRI paradigm involving trait-judgment for known others was utilized; findings were, therefore, inherently reflective of this specific manner in which participants were asked to bring to mind their close others. As recognized in Chapter 2, a trait judgment task like this is only one of many potential tasks that can effectively examine neural representations of close others using fMRI. Future studies could draw upon paradigms designed and tested by past work, such as the induction of threat accompanied by actual or simulated presence of attachment figures (e.g., Coan, Schaefer, & Davidson, 2006; Eisenberger et al., 2011). Researchers should also consider designing new tasks fundamentally grounded in the tenets of attachment theory. As one example, participants could be asked to engage with a virtual social reality, wherein they have to make decisions to interact with their environment in a manner behaviorally similar to "exploration". Throughout the experiment, decision-making could be systematically paired with sensory cues of relationship partner presence. This type of paradigm could be tested by an event-related fMRI design and would still have great ecological validity.

Future research could also combine methods from the social psychological and human neurobiological traditions to gather more nuanced information about participants. Daily diary studies provide important self-report data detailing individuals' everyday interpersonal experiences (e.g., Selcuk et al., 2015). Double-blind placebo-controlled administration of important neurochemicals, such as intranasal oxytocin (e.g., Ditzen et al., 2009), remains a gold standard for testing the direct manipulation of brain response to environmental stimuli. Chapters 3 and 5 demonstrated that there exist unique neural signatures of some of our most salient attachment figures — romantic partners and parents/children, respectively. This line of research

would greatly benefit from dyadic or "couples" studies, wherein data are collected from both members of a partner pair. Combining this method with fMRI techniques, for example, could shed light on affective coregulation within attachment bonds and its relationship to patterns of functional brain activity. Investigations of dyads would also allow for assessment of biobehavioral synchrony (see Feldman, 2016 for review), and this research could be further extended to examine neural synchrony using correlational methods from social-cognitive neuroscience (e.g., Dikker et al., 2014; Hasson et al., 2004).

Implications for Well-Being and Health in Normative and Clinical Populations

It is well-documented that close relationships in adulthood have profound effects on overall well-being and health (Carstensen et al., 1996; Cohen, 2004; Cornwell & Waite, 2009; Hoppmann & Gerstorf, 2009; House, Landis, & Umberson, 1988; Kiecolt-Glaser & Newton, 2001; Steptoe et al., 2013). However, relatively little research to date has been devoted to investigating the neural and cognitive representation of such bonds throughout the life course. Chapter 4 directly focuses on the effects of aging on neural representations of known others, along a spectrum of closeness and attachment. Future research should maintain this developmental focus and seek to cover all periods of the lifespan. This line of work could include longitudinal studies of individuals and their dynamic close relationships across time, as some have begun to examine (Xu et al., 2012). Another avenue for future work that is more translational in nature would involve promoting social connectedness and health behaviors (Umberson et al. 2010) as fundamental components of brain health into older adulthood. Also, research investigating brain activity for parents and children, as in Chapter 5, could serve to inform the public of the cognitive benefits for children of responsive parenting practices (Feldman, 2012). Ideally, future work on these topics will also have the resources to sample

more inclusively from vastly understudied populations, such as individuals who identify with gender, sexual orientation, and racial minorities, as well as clinical and non-normative populations. Future research across the fields of psychology, sociology, and human neuroscience could certainly shed light on the universal health and psychological benefits of chronically accessible attachment figure mental representations.

Concluding Remarks

Integrating ethological attachment theory with current fMRI methods, the present studies systematically investigated the neural representation of close relationship partners across adulthood. Collectively, these results make an important contribution to our growing understanding of just how significant our closest relationships can be, at the level of physiology. Past research has already demonstrated that, as part of attachment bonds, close others become integrated into one's sense of self (Aron et al., 1991) and "under [one's] skin" (Pietromonaco, DeBuse, & Powers, 2013). Findings from the present studies assert another critical layer—that of unique neural representation—to these important processes of close relationship formation and maintenance.

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Appendix 2.A.

Relationships and Brain Function Study

Please complete the following brief survey at least 24 hours in advance of your scanning session.

Important People in Your Life

Below you are asked to list people who are significant in your life. Rather than providing their names, answer with a term that defines how they are related to you (e.g., mother, boyfriend, sister). If you write in more than one person, *list them in order of significance*, starting with the most significant.

Note:
1. Please DO NOT use terms like "family" or "friends" that refer to more than one person.
2. If you are including more than one "friend"/"housemate"/etc. on your list, please specify which individual you are referring to (i.e., friend1, friend2, and so on).
3. There is no need to fill in all of the boxes.

1. **Person(s) who should be contacted in case of an emergency involving you.**

A:

B:

C:

D:

2. Person(s) whose absence make you feel like something is not quite right.

A:

B:

C:

D:

3. Person(s) you are most likely to tell when something good happens to you.

A:

B:

C:

D:

4. Person(s) you can hardly imagine your life without.

A:

B:

C:

D:

5. Person(s) you immediately think of contacting when something bad happens.

A:

B:

C:

D:

6. Person(s) you know always want the best for you.

A:

B:

C:

D:

7. Person(s) you know will always be there for you.

A:

B:

C:

D:

8. Person(s) you make sure to see or talk to frequently.

A:

B:

C:

D:

9. Person(s) you miss when they are away.

A:

B:

C:

D:

10. Person(s) you seek out when worried or upset.

A:

B:

C:

D:

The following questions are relevant to your **romantic partner.**

1. **What is your partner's first name?**

2. **How long have you been in a relationship your partner? Please give answer in number of months:**

For the below questions, please put an "X" next to the option that reflects your response:

How well would you say you know your partner?

not at all well _____
slightly well _____
somewhat well _____
moderately well _____
extremely well _____

How familiar are you with your partner?

not at all familiar _____
slightly familiar _____
somewhat familiar _____
moderately familiar _____
extremely familiar _____

To what extent would you consider your partner to be influential in your life?

not at all influential _____
slightly influential _____
neutral _____
moderately influential _____
extremely influential _____

How emotionally invested in your partner would you say you are?

not at all invested _____

slightly invested _____

somewhat invested _____

moderately invested _____

extremely invested _____

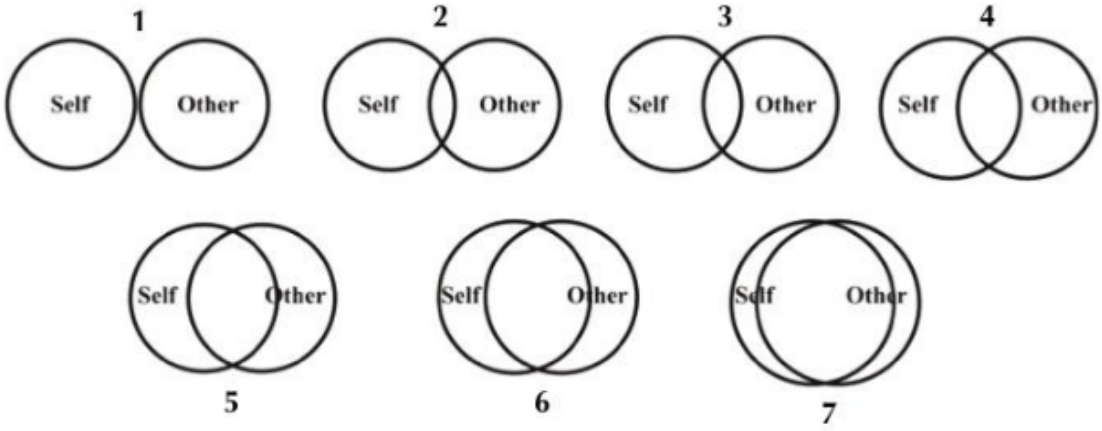
Please respond to the following items with your romantic partner in mind. For each item/row please place an "X" in the box that reflects your response.

	Strongly Disagree	Disagree	Neither Agree nor Disagree	Agree	Strongly Agree
I feel our love is based on a deep and abiding friendship.					
I express my love for my partner through the enjoyment of common activities and mutual interests.					
My love for my partner involves solid, deep affection.					
An important factor in my love for my partner is that we laugh together.					
My partner is one of the most likable people I know.					
The companionship I share with my partner is an important part of my love for him/her.					
I feel I can really trust my					

partner.					
I am able to count on my partner in times of need.					
I feel relaxed and comfortable with my partner.					

We are interested in learning more about your relationship with your romantic partner. Below are pairs of circles. In each pair, one circle represents you and the other circle represents this person. **Please put an "X" next to the number that corresponds with the pair of circles best describing your relationship.**

1 ____
2 ____
3 ____
4 ____
5 ____
6 ____
7 ____



The following statements concern your feelings about your current romantic partner or your current romantic relationship. For each item/row please place an "X" in the box that reflects your response.

	not at all	slightly	somewhat	neutral	moderately	very	extremely
How committed are you to your current romantic relationship?							
How sexually exclusive is your current romantic relationship?							
How satisfied are you with your current romantic relationship?							
How satisfied are you with your current romantic partner?							
How attracted to this person are you?							

Please indicate how much you agree or disagree with the following statements regarding your romantic partner. **For each item/row please place an "X" in the box that reflects your response.**

	Strongly Disagree	Disagree	Somewhat Disagree	Neither Agree nor Disagree	Somewhat Agree	Agree	Strongly Agree
Every little thing reminds me of this person.							
My friends probably think I talk about this person too much.							
I have to stop myself from talking about this person all the time.							
I spend a lot of time analyzing everything this person says and does.							
I am always trying to figure out how this person feels							

about me.							

For each item/row please place an "X" in the box that reflects your response.	Not at all true (1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	Definitely true (9)
I would feel deep despair if my partner left me.									
Sometimes I feel I can't control my thoughts; they are obsessively on my partner.									
I feel happy when I am doing something to make my partner happy.									
I would rather be with my partner than anyone else.									
I'd get jealous if I thought my partner were falling in love with someone else.									

I yearn to know all about my partner .									
I want my partner physically, emotionally, mentally.									
I have an endless appetite for affection from my partner.									
For me, my partner is the perfect romantic partner.									
I sense my body responding when my partner touches me.									
My partner always seems to be on my mind.									
I want my partner to know me--my thoughts, my fears, and my hopes.									
I eagerly look for signs indicating my									

partner ’s desire for me.									
I possess a powerful attraction for my partner.									
I get extremely depressed when things don't go right in my relationship with my partner.									

Please take a moment to think about how you feel, think, and behave in your current romantic relationship. The items below refer specifically to your feelings in relation to your current romantic partner. Using the rating scale provided, indicate how much you agree/disagree with each statement listed below. **For each item/row please place an "X" in the box that reflects your response.**

	Strongly Disagree	**Disagree**	**Somewhat Disagree**	**Neutral /Mixed**	**Somewhat Agree**	**Agree**	**Strongly Agree**
I worry that my partner thinks that I don't measure up to other people.							
I feel comfortable sharing my private thoughts and feelings with my partner.							
I worry a lot about my relationship with my partner.							
I find it difficult to allow myself to depend on my partner.							
I often worry that my partner doesn't really love me.							

I am very comfortable being close to my partner.							
I worry that my partner doesn't care about me.							
I don't feel comfortable opening up to my partner.							
My partner makes me doubt myself.							
I prefer not to show my partner how I feel deep down.							

The following questions are relevant to your **mother/father OR child.**

Please choose the parent or child to whom you feel closest.

1. What do you normally refer to this parent or child as (e.g. "mom", "dad', child's name)?

2. How well would you say you know this parent / child?

- not at all well ___
- slightly well ___
- somewhat well ___
- moderately well ___
- extremely well ___

3. How familiar are you with this parent / child?

- not at all familiar ___
- slightly familiar ___
- somewhat familiar ___
- moderately familiar ___
- extremely familiar ___

4. To what extent would you consider this parent / child to be influential in your life?

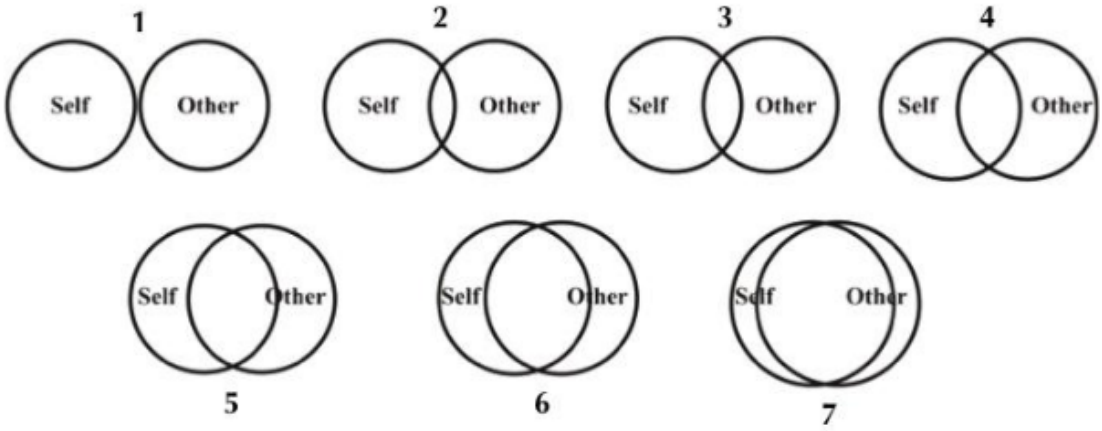
- not at all influential ___
- slightly influential ___
- neutral ___
- moderately influential ___
- extremely influential ___

5. How emotionally invested in this parent / child would you say you are?

- not at all invested ___
- slightly invested ___
- somewhat invested ___
- moderately invested ___
- extremely invested ___

We are interested in learning more about your relationship with your **parent / child, as specified above.** Below are pairs of circles. In each pair, one circle represents you and the other circle represents this person. Please choose the number that corresponds with the pair of circles best describing your relationship.

1 ____
2 ____
3 ____
4 ____
5 ____
6 ____
7 ____



Please think of a close friend of yours who is the same gender as you are. This person should be someone you have a current, positive (non-romantic) relationship with. If possible, try to think of a friend you have known for about as long as you have known your romantic partner, named above.

The following questions are relevant to **this close friend.**

1. What is your close friend's first name?

2. How long have you known and interacted with your close friend? Please give answer in number of months.

3. How well would you say you know your close friend?

- o not at all well ___
- o slightly well ___
- o somewhat well ___
- o moderately well ___
- o extremely well ___

4. How familiar are you with your close friend?

- o not at all familiar ___
- o slightly familiar ___
- o somewhat familiar ___
- o moderately familiar ___
- o extremely familiar ___

5. To what extent would you consider your close friend to be influential in your life?

- not at all influential ___
- slightly influential ___
- neutral ___
- moderately influential ___
- extremely influential ___

6. How emotionally invested in your close friend would you say you are?

- not at all invested ___
- slightly invested ___
- somewhat invested ___
- moderately invested ___
- extremely invested ___

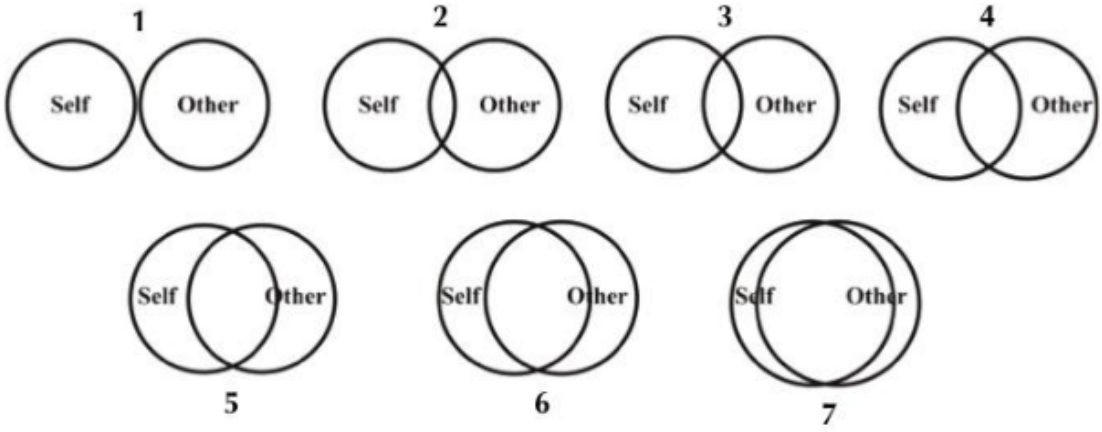
Please respond to the following items with your close friend in mind. **For each item/row please place an "X" in the box that reflects your response.**

	Strongly Agree	**Agree**	**Neither Agree nor Disagree**	**Disagree**	**Strongly Disagree**
I feel our love is based on a deep and abiding friendship.					
I express my love for my friend through the enjoyment of common activities and mutual interests.					
My love for my friend involves solid, deep affection.					
An important factor in my love for my friend is that we laugh together.					
My friend is one of the most likable people I know.					
The companionship I share with my friend is an important part of my love for him/her.					
I feel I can really trust my friend.					

I am able to count on my friend in times of need.					
I feel relaxed and comfortable with my friend.					

Q268 We are interested in learning more about your relationship with your **close friend**. Below are pairs of circles. In each pair, one circle represents you and the other circle represents this person. Please choose the number that corresponds with the pair of circles best describing your relationship.

1 ____
2 ____
3 ____
4 ____
5 ____
6 ____
7 ____



Please think of a familiar acquaintance of yours. This person should be someone who plays a neutral, minor role in your life. Again, try to pick someone that you have known for about as long as your romantic partner and close friend but is significantly less close to you.

The following questions are relevant to **this familiar acquaintance.**

1. What is your familiar acquaintance's first name?

2. How long have you known and interacted with your familiar acquaintance? Please give answer in number of months.

3. How well would you say you know your familiar acquaintance?

- not at all well ___
- slightly well ___
- somewhat well ___
- moderately well ___
- extremely well ___

4. How familiar are you with your familiar acquaintance?

- not at all familiar ___
- slightly familiar ___
- somewhat familiar ___
- moderately familiar ___
- extremely familiar ___

5. To what extent would you consider your familiar acquaintance to be influential in your life?

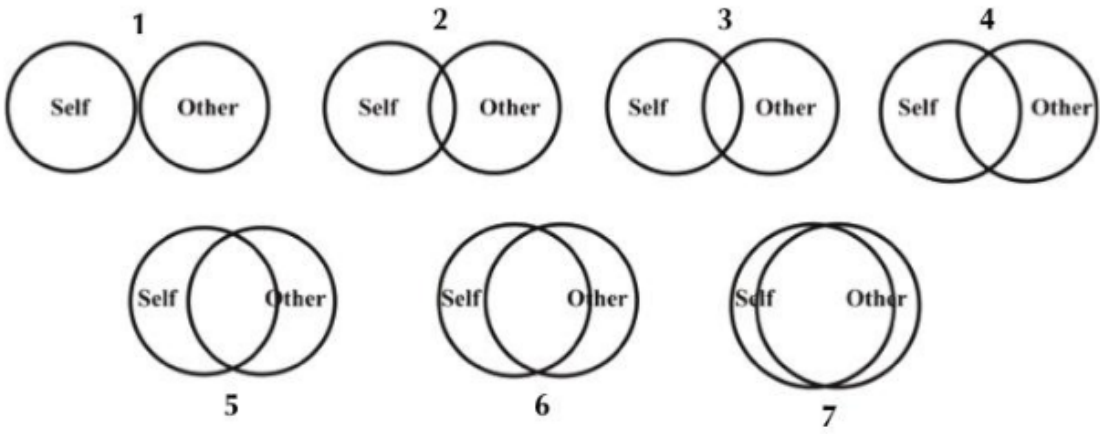
- not at all influential ___
- slightly influential ___
- neutral___
- moderately influential ___
- extremely influential ___

6. How emotionally invested in your familiar acquaintance would you say you are?

- not at all invested ___
- slightly invested ___
- somewhat invested ___
- moderately invested ___
- extremely invested ___

We are interested in learning more about your relationship with your **familiar acquaintance.** Below are pairs of circles. In each pair, one circle represents you and the other circle represents this person. Please choose the number that corresponds with the pair of circles best describing your relationship.

1 ____
2 ____
3 ____
4 ____
5 ____
6 ____
7 ____



Please think of a famous person of the opposite gender, and fill in his or her name here:

_____

Thank you for completing this portion of the study!

Please enter your participant number (emailed to you) in the box below.We will see you for your session in the scanner soon.

Participant ID number:

Appendix 3.A.

Name Prompts for Each Condition

Romantic partner: “What is your partner’s first name?”

Parent: “Please choose the parent to whom you feel closest. What do you normally refer to this parent as (e.g. ‘mom’, ‘dad')?”

Close friend: “Please think of a close friend of yours who is the same gender as you are. This person should be someone you have a current, positive (non-romantic) relationship with. If possible, try to think of a friend you have known for about as long as you have known your romantic partner, named above.”

Familiar acquaintance: “Please think of a familiar acquaintance of yours. This person should be someone who plays a neutral, minor role in your life. Again, try to pick someone that you have known for about as long as your romantic partner and close friend but is significantly less close to you.”.

Famous person: “Please think of a famous person of the opposite gender, and fill in his or her name here.”

Relationship Questionnaire (Partner)

The following questions are relevant to your **romantic partner.**

3. **What is your partner's first name?**

4. **How long have you been in a relationship your partner? Please give answer in number of months:**

How well would you say you know your partner?

not at all well _____
slightly well _____
somewhat well _____
moderately well _____
extremely well _____

How familiar are you with your partner?

not at all familiar _____
slightly familiar _____
somewhat familiar _____
moderately familiar _____
extremely familiar _____

To what extent would you consider your partner to be influential in your life?

not at all influential _____
slightly influential _____
neutral _____
moderately influential _____
extremely influential _____

How emotionally invested in your partner would you say you are?

not at all invested _____
slightly invested _____
somewhat invested _____
moderately invested _____
extremely invested _____

The following statements concern your feelings about your current romantic partner or your current romantic relationship.

	not at all	slightly	somewhat	neutral	moderately	very	extremely
How committed are you to your current romantic relationship?							
How sexually exclusive is your current romantic relationship?							
How satisfied are you with your current romantic relationship?							
How satisfied are you with your current romantic partner?							
How attracted to this person are you?							

Appendix 4.A.

Name Prompts for Each Condition

Romantic partner: “What is your partner’s first name?”

Parent / Child: “Please choose the parent or child to whom you feel closest. What do you normally refer to this parent as (e.g. ‘mom’, ‘dad’, child’s name)?”

Close friend: “Please think of a close friend of yours who is the same gender as you are. This person should be someone you have a current, positive (non-romantic) relationship with. If possible, try to think of a friend you have known for about as long as you have known your romantic partner, named above.”

Familiar acquaintance: “Please think of a familiar acquaintance of yours. This person should be someone who plays a neutral, minor role in your life. Again, try to pick someone that you have known for about as long as your romantic partner and close friend but is significantly less close to you.”.

Famous person: “Please think of a famous person of the opposite gender, and fill in his or her name here.”

Appendix 4.B.

List of Trait Adjectives

Shy	Forgiving
Modest	Quiet
Sociable	Curious
Stubborn	Talkative
Clever	Nervous
Unobservant	Diligent
Sympathetic	Irresponsible
Competent	Critical
Attentive	Bold
Argumentative	Comical
Persuasive	Easygoing
Distrustful	Persistent
Insecure	Irritating
Pleasant	Self-assured
Helpful	Impulsive
Emotional	Imaginative
Sarcastic	Friendly
Systematic	Fearful
Hot-tempered	Indecisive
Sincere	Practical
Moody	Energetic
Demanding	Forgetful
Thoughtful	Idealistic
Sensible	Gullible
Envious	Reliable